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EXPERIMENTS IN PROPAGATION OF FRESH-WATER MUSSELS OF THE QUADRULA GROUP

By ARTHUR DAY HOWARD

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INTRODUCTION.

The fresh-water mussels of central North America with their heavy shells of beautiful pearl are a natural resource the value of which probably has not begun to be realized. The extensive development of the pearl-button industry in a brief period of 20 years is evidence of the wealth of the original natural supply; but a very evident decrease of readily obtainable shells, along with the increasing necessity for extension of clamming operations to more and more distant sources of supply, has made it evident that this resource is not unlimited.

Within the first 10 years of the growth of the industry, interested manufacturers requested an investigation of conditions by the United States Bureau of Fisheries. The purposes of this first investigation (Smith, 1899, Simpson, 1899) were to discover whether indiscriminate and wasteful methods were being employed that might be corrected by supervision or restrictive legislation. Later there were carried on for a number of years investigations to determine if methods could be found for artificially supplementing the natural production of young mussels, i. e., methods similar to those so successfully employed by the Bureau in the culture of oysters, trout, lobsters, and other water forms of economic importance.

The essential facts in the life history of the fresh-water pearl mussels (Unionidæ or Naiades) have been known since the discovery by Leydig in 1866 that at one stage they are parasitic upon fishes. An historical account of these discoveries and the life history of fresh-water mussels, together with methods which have been adopted for their propagation, have been described in publications by the Bureau of Fisheries (Simpson, 1899, Lefevre and Curtis, 1912). The work in propagation, however, has been limited to a few species

of the *Lampsilis* group, chiefly *Lampsilis ligamentina* and *L. ano-dontoides*. With one possible exception, none of the *Quadrula* group of mussels, including some of the most valuable commercial shells, had been, up to the time of the present investigation, carried through the parasitic stage, though many experiments had been made on various species of fish and under varied conditions to determine a suitable method of propagation. The rarity of successful infections, along with other indications, suggests that, as in other cases of parasitism in the animal and vegetable kingdom, each mussel may have its appropriate host or hosts restricted to a species of fish, a genus or a family, as the case might be, and that the reason for failure was due to not finding the proper host.

Since the number of species of mussel for this locality (Fairport, Iowa) is 40 or more and the number of species of fairly common fish at least 60, the problem of determining the appropriate host for each mussel is obviously quite complex. To determine the hosts for each species of mussel by artificial infection, a "trial and error" method would be roundabout and difficult. Obviously a more direct solution of the problem, as I have shown in a previous paper (Howard, 1912), would be secured by a study of natural infections, i. e., fish taken at large are examined for glochidia and when present these are determined as to species, condition, etc. In the present investigation of some of the *Quadrula* group of mussels the above method was the one chiefly employed. Studies were begun in February, 1912, upon assignment of the problem by the director, Dr. R. E. Coker, at the Government biological laboratory at Fairport, Iowa.[a]

METHODS AND TECHNIQUE OF EXPERIMENTS.

As stated above, the matter of first importance in determining how to propagate a given species of mussel seemed to be the finding of a suitable host. In making this search I have examined as many local species of fish as were obtainable, identifying, if possible, all glochidia found upon the gills or fins. Some glochidia, because of peculiarities of form or size, were readily determined, while others were less easily identified because of fewer apparent differences. In this study I have made identifications by comparison of the glochidium found in the natural infections with a series of preparations and drawings of glochidia (see Surber, 1912) obtained from gravid mussels.

Fishes were examined for natural infections wherever obtainable, but attention was also given to securing them in the vicinity of special mussel beds. Infected filaments of gills or portions of fins have been examined and drawn, first in the fresh state and then fixed

in 10 per cent formalin or a one-third saturated solution of bichloride of mercury. The usual histological procedure for whole mounts was followed after fixation. Acid fixing fluids and acid stains have been avoided on account of the delicate calcareous shells of the glochidia. For the sake of accurate comparison in identifications it has seemed desirable to apply the same method of preparation for the natural infections that is used for the glochidia.

When evidence of the natural host was obtained by the above method, the kind or kinds of fish thus designated were tested by artificial infection to verify the results already secured and to determine the possibilities of artificial propagation.

The method of making artificial infections is as follows: Young mussels or glochidia, which are produced to the number of many thousands by each female mussel, are taken from the gill of the latter and placed in a receptacle with the fish to be infected. The myriads of glochidia thus distributed through the water, passing constantly through the gill openings of the fish, become attached to the filaments of the gills or in some cases fasten externally upon the fins. As soon as they become attached there is a reaction of the tissue in the nature of an hypertrophy of the external epithelium which produces a cyst enveloping the glochidium.

For a fuller discussion of infection methods I would refer to the paper by Lefevre and Curtis (1912). Some special difficulties encountered in dealing with the short-period breeding *Quadrulas* will be discussed in connection with the propagation of *Quadrula pustulosa* and artificial infection of *Quadrula ebena*.

Glochidia were obtained from gravid mussels collected with the "crowfoot" and mussel rake, the usual methods in vogue among clammers. The preparation of these was for the most part by the method described by Surber (1912). For differentiating the thread gland, Grenacher's borax carmine was employed as a stain. Examinations in alcohol covered to prevent evaporation gave better differentiation for some features than the stained and cleared material.

The collection of juveniles has been carried on chiefly by two methods—dredging and hand or shore collecting. The dredge employed was of the Chester rake pattern and of suitable dimensions for use with a gasoline launch. This method is adapted for deep water or for shallow water that is so muddy as to make it impossible to see the bottom. As the Mississippi has been almost constantly muddy during the warmer months this method has proved to be the chief reliance. The small shells are separated from sand and mud by means of a sieve or by washing in a fine-meshed bag. Hand collecting was about the only method applicable to very shallow water and stony bottom, and was employed during winter or on very rare occasions in summer when the water was sufficiently clear.

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DETAILS OF OBSERVATIONS.

In the following account, the experiments and observations have been described under the name of each species. This was done for the sake of clearness and convenience, and it will be readily seen that all have not received equal attention. I have followed chiefly the classification and nomenclature of Simpson (1900), in places employing Ortmann's system, in which case it is so indicated. The changes made by Ortmann, so far as they apply to the forms I have considered, seem justified. These are based, according to that author, upon a thorough study of the anatomical characters of the soft parts as well as of the shell. It seems evident enough that a continuance of this kind of revision is very desirable. In this I make no criticism of the herculean labors of Simpson, whose synopsis has removed the taxonomy of the Naiades from chaos.

I have described and figured some of the glochidia in order to bring out features not previously considered, while others previously published are reproduced in order to show all on the same scale. In the dimensions the "height" signifies the longest axis perpendicular to the hinge line, while the "length" is the longest axis parallel to the hinge line. The range given for each dimension is the extent of variation that I have observed. The greatest that I have measured was 12 per cent. If the measurements had been taken from several broods of glochidia from different localities, this variation would probably be larger.

Very little has been published regarding the juvenile stages of the *Quadrulas*. It is not my intention to go into details of description here, reserving such observations for a later paper; however, a few notes are given by way of calling attention to this little-known stage. I regard a knowledge of these as necessary for a proper consideration of the problems connected with the propagation of mussels. If the suggestion (Lefevre and Curtis, 1912, p. 192) that propagation be carried through this stage prove to be feasible, such information would be indispensable. Again, a knowledge of these is required for the maintenance of proper conditions for the natural development of mussel beds. From the few observations that have been published upon juveniles of North American Unionidæ (Isely, 1911; White, 1905; Sterki, 1891 a, b), it seems probable that, in some cases at least, they have a habitat quite different from the adult. For example, some species, such as the yellow sand-shell, *Lampsilis anodontoides*, and the butterfly, *Plagiola securis*, have been found in the shallow water of rapids or riffles attached to stones or gravel by a byssus, while the adult dwells in deep water on a mud or sand bottom. Differences so great between the habitat of the young and the adult would be important considerations in any attempt to raise mussels artificially through this stage.

THE WARTY-BACK, *Quadrula pustulosa* (Lea). [Pl. i, fig. 1, 2.]

This mussel, with allied species, is commonly called the warty-back and pimple-back because of the pustules on the shell. It is a shell of good luster and texture, and therefore is ranked high by manufacturers.

Distribution.—Its range is throughout the Mississippi drainage and into Michigan, extending east into the Alabama River system and west into central Texas.

Habitat.—It is found in streams of some size either in gravel or on mud bottom (Scammon, 1906).

Juvenile.—The juvenile, of 10 to 20 mm. in length, can be recognized by a broad triangular green ray upon the lateral slope. I have found it chiefly in fine gravel or sand in a strong current.

No byssus was observed in a considerable number of specimens taken and none has been reported for this species to my knowledge; apparently, however, there is a byssus gland present. In the very early stages (less than 1 mm. in length) a mucilaginous secretion is produced which serves to anchor the young mussel. I think it doubtful if this species at any stage produces the hard hyaline byssus threads which are found in some of the Lampsilinæ. Among the *Quadrulus* here described the only case of a true byssus observed was in that of a specimen of *Q. plicata* having a length of 4.5 mm.

Glochidium (pl. v, fig. 36).—The warty-back is a summer breeder, or tachytictic, the glochidia being found during the months of June, July, and August. The earliest record that I have for a season is June 12, and the latest August 23, when I found two gravid out of 46 examined. The glochidia occupy all four gills in the female, and are white in color. They are of the hookless type, and as seen flatwise, the usual position for examination under the microscope, have the form of an elongated purse (pl. v, fig. 36).

Dimensions: Height, 0.28 mm. to 0.3 mm.; length, 0.22 mm. to 0.23 mm.; length of hinge line, 0.08 mm., or 2.75 times in length. The difference in height observed (0.28 mm.–0.3 mm.) gives a variation of less than 8 per cent; more than 10 per cent seems to be uncommon in glochidia of one species, although I have seen 12 per cent. This species should not be confused with any others in the region investigated because of unique form and size. The only glochidia here at all resembling it are those of *Lampsilis luteola* and *Plagiola securis*. *L. luteola* can be distinguished by its relatively greater width (0.25 mm.) and hinge line (0.118 mm.), and *Plagiola securis* by its greater length (0.31 mm. to 0.33 mm.) and different proportions.

Natural infection.—The first record for a natural infection by this species was found upon a catfish obtained July 5. This was the channel cat, *Ictalurus punctatus*, and was the first record of infection

found on catfishes. Previous to that time all examinations of cat-
fishes had favored the belief that they were immune to all glochidial
infection. Other records for this fish were obtained through July
and August, the breeding period for the mussel. The fish were taken
by seining over known shell beds in one instance, in others in wing
nets and bait nets of commercial fishermen. In all, during 1912, 17
records of infection were obtained out of 39 fish examined, and 9 of
these were determined as *Q. pustulosa.*

This glochidium is more readily identified in infections than some
others, because of its large size and owing to its peculiar shape. None
of the mussels of similar dimensions have the same form. The nearest
approach to it is *Lampsilis luteola.* (See description of glochidium
above.) The glochidia in infection were usually well encysted, and
in many cases development was far advanced, even to the extent of
some growth beyond the glochidial shell. (Pl. iii, fig. 19, 23.)
This development of an extra embryonic shell in the parasitic
stage has been reported (Coker and Surber, 1911) for the *Proptera*
(Ortmann, 1912) group, but not, I believe, among the *Quadrulas.*
One record only was obtained of *Q. pustulosa* on another fish, the
yellow cat, *Leptops olivaris*, but this was important, as it suggested a
possible host for this mussel, and led to the discovery of many infec-
tions in *Ictalurus punctatus*, although one had been seen in that
species before. In 9 other specimens of *L. olivaris* examined by me
and 44 by Mr. T. Surber in August, no infections were found. From
the standpoint of natural infections, *I. punctatus* is indicated as the
natural host for *Q. pustulosa*, with a possible extension to other
species of the *Siluridæ.* After August 28 and during the autumn no
natural infections were obtained from a total of 98 fish examined.
This date corresponds with the latest date for gravid mussels of the
species. On August 23, 2 gravid shells were secured from a total of
48. After this date none were found in a total of 176 examined. This
gives a space of five days after the last gravid mussels were found,
during which the natural infections were obtained The indications
from this are that the parasitic period is brief. If the parasitic
period were a long one, say a month, this correspondence of dates
would be lacking.

The character of the cysts and their position on the gill filament
are features to which attention has been called as of importance, per-
haps, in determining the possibilities of artificial infection. The
cysts of *Q. pustulosa* on *Ictalurus punctatus* are of ordinary size. They
are often set off by a slight furrow or indentation (see pl. iii, fig. 23),
which is quite characteristic. The position is chiefly on the edge of
the filaments, often near the base, a rather unusual location. Lefevre
and Curtis (1912) are of the opinion that those fish in which the
glochidia are distributed on the tips of the filament are able to carry

a much greater number. An attachment near the base of the fila-ment giving a more intimate relation with the host may insure more certain survival to the glochidium. However, the cysts I have examined gave no evidence of serious interference with circulation in the filament, so it looks as if the position in the case of the catfish probably would not make much difference in the effect on the host.

The finding of glochidia on the catfishes is of interest, since this fish had been regarded as belonging to the immune class, this opinion being based largely on the results of artificial infection. The habits of the fish as a bottom feeder, and especially as a voracious eater of mussels, would make it seem surprising if it did not carry the glo-chidia of some species of mussel. Forbes and Richardson (1908), in examination of the food of these fish, say:

Mollusks, about equally large water snails, and large, thin clams were a decidedly important element, being found in 15 of the 43 fishes. They amounted to 15 per cent of the food of the group, and several specimens had little or nothing else. Notwith-standing the number of bivalves eaten by this fish, no fragment of a shell was ever found in their stomachs, but the bodies of the mollusks seem to have been separated while yet living from the shells, as indicated by their fresh condition and by the fact that the shell muscles were scarcely ever present.

TABLE 1.—ARTIFICIAL INFECTIONS WITH QUADRULA PUSTULOSA.

Date.	Ex-peri-ments.	Species of fish.	Num-ber of fish.	Number of glo-chidia attach-ing.	Date liberated.	Period on fish.	Develop-ment at latest observa-tion.	Aver-age tem-pera-ture.
1912. Aug. 21	V–22	Ameiurus melas	6	88.......	Aug. 27–29..	6 to 8 days..	Complete	°F. 75.1
23	V–26	.....do.................	2	230......	....	More than 8 days.	...do.....	75.5
1913. June 12	VI–1	Ameiurus {melas .... {nebulosus ...}	7	500......	June 27–29..	15 to 17 days.	....do....	72.1
24	VI–4	L. olivaris (wt. ½ lb.)...	1	Many...	....	11 days.......	Advanc-ed.	78.3
24	VI–4	L. olivaris (wt. 2½ lbs.).	1	...do.....	....	9 days or less..	...do.....	
July 7	VI–10	Ictalurus punctatus....	8	...do.....	July 16–18...	9 to 11 days..	Complete	78.1
10	VI–12	.....do................	10	...do.a...	July 20–21...	10 to 11 days.	...do.....	76.7
10	VI–12	Lepomis pallidus.......	2	Several..	July 11......	1 day........	None....	
10	VI–12	Pomoxis sparoides.....	2	Very few	.....do......	.....do......	...do.....	
10	VI–12	Pomoxis annularis.....	3	...do.....	.....do......	.....do......	...do.....	
29	VI–19	Ictalurus punctatus....	1	Many....	Aug. 8......	10–12 days...	Complete	76.3
29	VI–19	Aplodinotus grunniens.	1	Few....	July 29–30...	1 day........	None....	
29	VI–19	Leptops olivaris........	1	Several..	Aug. 6–8....	8 to 10 days..	Complete	
29	VI–19	Pomoxis sparoides.....	2	None....	....			
29	VI–19	Micropterus salmoides..	1	Many....	July 31......	1 day........	None....	
Aug. 4	VI–20	Ictalurus punctatus....	29	...do.....	Aug. 15–16..	11 to 12 days.	Complete	75.5
4	VI–20	Leptops olivaris........	3	...do.....	Before Aug.9	Less than 5 days.	?........	76

a On gills and barbels. All other glochidia were attached to gills only.

As *Q. pustulosa* is a heavy-shelled species it may not supply the catfish with food by way of returning favors, unless the fish has some means of opening the heavy shells. However, as mussels of various species segregate in the same location, forming beds, the thinner-shelled species in furnishing food to the fish would favor the

breeding of the heavier-shelled species. This attraction of the fish would serve to furnish the host and also increase the chances of the young mussels being shed there by the fish, thus partly accounting for the segregation of mussels. The fishermen on the Mississippi take advantage of this appetite in the catfish by baiting nets with the "meats" of the mussels which the clammers or mussel fishermen remove from the shells.

Artificial infection.—The finding of glochidia of *Q. pustulosa* on catfishes in natural infection suggested testing these fishes in experiments in artificial infection.

In these experiments four species of catfish were tried and five other kinds of fish. The results of some of these experiments are shown in table 1.

When exposed to infection in the same tank and thus under the same conditions, the difference in susceptibility between the catfish and the other species was very marked and the difference in implantation still more so. The catfish in general received them more quickly and retained the glochidia, while, though abundant on the gills of some of the other species, they disappeared before the end of the second day.

The results in the case of the different species of catfish were not uniform. The duration of the parasitic period seems to vary slightly in the different species and there is evidence of immunity in some individuals of *Leptops olivaris*. The greatest variation in duration of parasitism occurred in the case of the bullheads *Ameiurus melas* and *A. nebulosus*. (See table 1, experiments V–22 and VI–1.) The long period, 17 days, can be explained by the lower temperature (average 72.1° F.); but the temperature of 75.1° F. for the shorter period of 6 to 8 days is no higher than those in which the parasitism is of much longer duration.

The experiments with *Ictalurus punctatus* gave more definite and regular results than with any of the other species. The majority of the experiments were conducted between June 18 and August 14, during a season when the water temperatures were more uniform than usual. This probably accounts for the uniformity in the parasitic period, which was determined as 9 to 12 days. The minimum period on a fish is less readily determined than the maximum; taking this into account it is probable that the period may be less than 9 days for some. This seems a remarkably short period when we consider cases of winter-breeding mussels carried over six months by the fish.

The young mussels after dropping from the fish were secured and their structure and habits noted.[a]

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[a] During these early stages I observed cases of ingestion by a turbellarian very abundant in the aquarium. This, with the number of empty shells found, indicates a high mortality among them.

The growth of shell, according to my observations, was quite rapid for the first few days; at two weeks it was nearly twice as long as the glochidium; at four weeks no increase was observed beyond that of the second week. This cessation of growth is rather surprising, but is in accord with many observations upon growth under laboratory conditions. Just what is the cause of this inhibition of growth I can only surmise. The young mussels were kept in aquaria having a constant stream of running water coming from the river, their natural habitat. It is quite likely that under these conditions the water contains too small an amount of suitable food material. A further discussion of this matter and a more detailed account of the early juvenile stages I will reserve for another paper.

The evidence of immunity in *Leptops olivaris* will be seen by a comparison of results (see table 1) in experiments VI–4 and VI–20. In the latter the glochidia were all shed in less than 5 days, and thus in all probability did not reach maturity. In experiment VI–4 the small individual carried a large number for 11 days, the usual period of parasitism, while the larger fish on the ninth day had one glochidium only.

This indication of occasional or even common immunity to these glochidia in *L. olivaris* is suggested in studies of natural infections, as I have already shown. The fish is rarely found infected in nature by any mussel, and I have only two records of infection by *Q. pustulosa*. In comparison with this, the abundant infection of *Ictalurus punctatus* (sometimes as high as 50 per cent in a catch) forms a marked contrast and with the foregoing experiments point conclusively to the channel cat as the usual host fish and the most suitable for artificial propagation.

Tests for optimum infection have been made which indicate that a smaller number of glochidia per fish is desirable than in the infections with the "mucket" mussel, *L. ligamentina*. The glochidia in the case of *Q. pustulosa* are considerably larger and the infection must necessarily be made at a season of the year when there is more danger of parallel infection with fungus (i. e., *Saprolegnia*). An infection of 800 to 1,000 glochidia is recommended for a fish of 1 pound weight, 1,500 to 2,000 for a fish of 2 pounds weight, and proportionate numbers for other sizes. Undoubtedly fish released in their natural waters would carry larger infections than those subjected to the more severe conditions of experimentation in captivity. In the foregoing estimates I have taken account of this.

The collection of gravid mussels of this species for artificial propagation requires the taking of some special precautions to prevent the premature discharge of the glochidia. The best results are secured in warm weather with mussels that have been collected the same day and a short time before the infections are to be made. If the edge

of the mantle and shell are uninjured, the gravid mussel may be kept alive out of water several hours, and still longer when kept cool. Mussels caught by the "crowfoot" method are more difficult to keep because of breaks in the shell.   It is difficult to prevent abortion of glochidia when a number of mussels are placed together in water even though running as from a tap or when the mussels are placed in crates in a river.   On account of this habit of abortion in *Q. pustulosa* and most of the *Quadrulas*, their transportation and retention is more difficult than in the case of the "mucket," *Lampsilis ligamentina*, and the other members of the Lampsilinæ that have been propagated artificially.   In the latter the portion of the gill differentiated for a marsupium is relatively so small that the breathing function of the gill is little interfered with by the presence of the embryos, while in the former the presence of glochidia in all four gills is probably responsible for this reaction when proper aeration is interfered with by crowding or otherwise.

Propagation.—This species of warty-back is one of the most valuable of the pearly mussels used in the button industry, so that any practical means of increasing the supply would be welcomed.   The determination of the host fish furnishes the means of employing the method of propagation that has proved so successful in the case of *Lampsilis ligamentina* and others of that genus.

In the catfish we seem to have a fish almost ideal for the application of this method.   It is abundant and hardy, thus meeting the conditions required by the method, i. e., the securing of many fish and the ability of the fish to withstand the handling and confinement incident to the process of infection with glochidia.   The method as employed for the past three years has had some modifications.   The fish, after seining, in one instance, were brought to a central station for infection; in the other they were infected in the field and immediately released.   Some fish will not survive even the latter very limited amount of handling or confinement; for example, the herring, *Pomolobus chrysochloris*, which has been determined as the host for the niggerhead, *Q. ebena* (Surber, 1913).   The power of catfish to survive removal from water is remarkable and this hardihood is an important feature, since the breeding period for these mussels is July and August, when the mortality is highest among fish in captivity.

A third modification of this method, the propagation of mussels in ponds or artificial streams after infection, may prove to be very practicable, as some mussels seem to prosper under these conditions.   If, in the case of the commercial species, this method proves successful it will offer the advantage of greater certainty in results.   By the method in use at present, the young mussel is released at a stage when it is quite at the mercy of its enemies and results are scarcely ascertainable.   If protected until a few millimeters long, when a heavy

shell has been formed, its chances of survival must be tremendously increased. The introduction of mussels into various streams when at this stage has been suggested (Lefevre and Curtis, 1912). This would have the advantage over the method of using the fish for distributing the mussel that transportation in the former case would be much easier and the fish can be used a second time. In this connection comes up the question whether a natural or an artificial distribution is better. It seems likely that conditions of introduction under control would be better then the probably haphazard distribution of young mussels in nature. When they drop off the gills of a fish their finding a favorable location is probably to a large extent a matter of chance. (See, however, discussion of segregation under head of natural infection, p. 11, 12.)

In the study of the juvenile mussels and their environment an attempt has been made to determine these conditions. For *Quadrula pustulosa* apparently a good current of water with proper food content and a bottom of fine gravel are demanded. The conditions of a pond are easier to meet, but the difficulties presented in producing the conditions of a flowing stream seem not to be insuperable.

The season of breeding is an important feature from the practical standpoint. The mussels of the short-breeding period are at some disadvantage because of the limited working season; this, however, is offset by the fact that during breeding months mussels and fish can more readily be obtained.

The number of glochidia per mussel is a feature of practical importance in propagation. As this species has an estimated average of about 200,000 or about one-fifth as many as the "mucket," *L. ligamentina*, it will be seen that a larger number of gravid mussels is necessary for a given number of fish to be infected. This small number as compared with some other species is somewhat offset by the abundance of the species.

THE PIMPLE-BACK, *Quadrula pustulata* (Lea). [Pl. VI, fig. 37, 38, 39.]

The quite similar *Q. pustulata* I have studied in the juvenile stage, finding it a habitant of sand bars, having 10 records for this location with only 2 for mud or gravel. The natural infections so far identified have been so few that little is known regarding this phase. I succeeded in artificially infecting the following fish with this species: *Pomoxis sparoides*, *Micropterus salmoides*, and *Lepomis pallidus*, but the death of the fish before the end of the experiment precluded the obtaining of any conclusive results. As the species is comparatively uncommon in this region its propagation would hardly be practicable here.

The glochidium has the following dimensions: Height, 0.25 mm.; length, 0.2 mm. (See Surber, 1912.)

THE PURPLE WARTY-BACK *Quadrula granifera* (Lea). [Pl. VI, fig. 40, 41.]

The shell of this species has purple nacre and is therefore not usually saved by clammers. The juveniles are very handsome because of the fine crenulations of the umbones. The glochidium is of large size having the following dimensions: Height, 0.355 mm.; length, 0.29 mm. (Surber, 1912.)

THE MAPLE-LEAF, *Quadrula lachrymosa* (Lea). [Pl. VI, fig. 43, 44.]

The odd sculpturing of this shell, with the coloring of the epidermis, makes it a handsome species. It seems not to be very common in the Mississippi in the region I have investigated, viz, between Hampton, Ill., and Muscatine, Iowa.

Distribution.—Western New York to Kansas and Minnesota, and south to Texas and Alabama. (Call.)

Habitat.—The larger lakes and rivers on a muddy or sandy bottom in somewhat shallow water. (Baker, 1898.)

Juvenile.—I have myself taken only a few juveniles of this species. These were found in shallow water in a rather swift current. The form is so much like the adult that it may be readily recognized.

Glochidium (pl. v, fig. 29).—Eggs were observed the middle of June; they were white in color and occupied all four gills. Early embryos of this species were found in four out of five specimens examined June 27. According to these observations, mature glochidia would be found during July in this region. Mature glochidia were obtained in August, 1912, from a tributary of Fall River, Glenwood County, Kans.,[a] and also June 12, 1913, at Fairport, Iowa. Form, of the purse-shaped type, similar to *Q. metanevra*.

Dimensions: Height, 0.085 mm.; length, 0.078 mm. This is the smallest glochidium of the *Quadrula* group that I have seen. Ortmann (1912) places *Tritogonia tuberculata* (Simpson) in the genus *Quadrula* on the basis of its anatomical structure. In its shell sculpture, though peculiar, he recognizes a relationship to the group of *Quadrula lachrymosa*. The extremely small size and similar form of the glochidia of these two species is another feature supporting this view.

Propagation.—No observations have been made upon natural infections. Experiments in propagation would be practicable in regions where the species is not uncommon. Scammon (1906) reports it abundant in Kansas and it is reported common in Indiana, and the closely allied species, *Q. fragosa* and *Q. nobilis*, are abundant in Arkansas.

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[a] I am indebted to Dr. Roy L. Moodie, of the University of Kansas, for this material.

THE MONKEY-FACE, *Quadrula metanevra* Rafinesque. [Pl. 1, fig. 4, 5.]

An odd shell of good luster and texture, but not of uniform thickness.

Habitat.—Larger streams and rivers, common in almost all stations. In my experience on the Mississippi it is found more often in the channel than on muddy bottom in still water.

Distribution.—Mississippi drainage area except its southern portion, extending to the Tennessee and Arkansas Rivers. (Simpson, 1900.)

Juvenile (pl. 1, fig. 6).—This stage was found on gravelly or sandy bottom in similar locations as the adult.

Glochidium (pl. v, fig. 31).—Form of the purse-shaped type with narrow hinge line. Dimensions: Height, 0.185 mm. to 0.2 mm.; length, 0.17 mm. to 0.176 mm. Breeding season, May, June, and July. This seems to be a short period and I suspect may be extended into August; however, examinations at the Fairport biological laboratory of some 89 specimens during August gave negative results.

Natural infection.—Infections with the glochidia of this mussel were found upon the gills of the sunfish, *Lepomis pallidus*, June 24, and of the sauger, *Stizostedion canadense*, July 26. The fish were taken at the edge of the river channel near mussel beds. Surber (1913) reports five infections on *Lepomis pallidus*. No decisive results in artificial infection with this species have been obtained, but the indications are that the sunfish, *L. pallidus*, may be infected successfully, and in the light of the information obtained regarding natural infections there should be no special difficulty in propagating this species.

THE NIGGERHEAD, *Quadrula ebena* (Lea). [Pl. 1, fig. 7, 8.]

This is a much-prized species because of the excellent luster, color, and texture of the shell, as well as its uniformity in thickness. Its habitat is both in mud and among rocks. Shells from a swift current have a better quality than those from water of little flow.

Distribution.—Mississippi drainage generally, except its western portion; Alabama and Tombigbee Rivers; northeast Texas? (Simpson, 1900.)

Juvenile (pl. 1, fig. 9).—The juvenile of this species I have taken only four times. Its scarcity in the collections is surprising when the abundance of the adult shell is considered. It seems probable that its habitat is on a pebbly bottom on which a dredge can scarcely pick up small material. Again, its color and shape are such as to make it difficult to find.

Glochidium (pl. v, fig. 30).—Gravid females with glochidia are reported from May until August. In 1912 the first found were 13 out of 85 examined on June 17, the latest 3 out of 66 examined on September 3. The spring of 1912 was late, which may have had the effect of delaying the breeding season.

All four gills are marsupial. The eggs are pink, giving this color to the gills. As development proceeds the embryos lose the color; but if, as is often the case, there are unfertilized eggs, the color remains until the eggs are discharged with the glochidia.

Form: Suborbicular; the outline as seen in side view is subsemi-circular. (Pl. v, fig. 30.)

Dimensions: Height, 0.148 mm. to 0.15 mm.; length, 0.153 mm. to 0.16 mm. The dimensions of this shell are so near those of *Q. trigona* and *Q. solida* that one is obliged to rely chiefly on the form to distinguish them.

Natural infection.—In seeking the natural host for this species the investigation was begun early in the spring; although infections at this time seemed improbable, it was necessary to determine whether any infections could be carried over winter. The results, so far as this species of mussel is concerned, were negative; but a common infection by another species was found in the sturgeon, *Scaphorhyn-chus platorhyncus*, early in April soon after the ice broke up. Mate-rial was obtained by seining and trammel nets as well as by fyke or wing nets and lines. Many natural infections of various species were found during the spring, but the first evidence of any infection resembling the glochidium of *Q. ebena* was obtained June 21 on *Micropterus salmoides*. This was a single glochidium; similar single infections were found in June on *Pomoxis sparoides*, and one August 9 on *Pomoxis sparoides*, and four the same date on *Pomoxis annularis*.[a]

With this limited evidence as a guide, experiments in artificial infection were tried upon the three species named. The tests, although giving some results of interest, did not indicate that the natural host had been found. A discussion of the results will be found under the next topic.

On August 13, while out with the station seining crew engaged in mussel propagation, Mr. T. Surber secured a specimen of the blue herring, *Pomolobus chrysochloris*, heavily infected with glochidia. These, upon examination, were determined to be *Q. ebena*. This was the first specimen of this species of fish known to have been taken this season during the breeding period of the niggerhead. Earlier in the spring, May 16, a specimen was brought to me which proved to be heavily infected, but not with the niggerhead.

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[a]The glochidia of *Q. ebena*, *Q. trigona*, and *Q. solida*, as will be seen by reference to the figures, do not differ greatly in appearance. This makes certain identifications difficult in some infections. (See *Q. plicata*, under natural infections, p. 27.)

Since finding this natural infection by the niggerhead, Mr. Surber has given special attention to the investigation of the infections by this mussel on the blue herring.   (See Surber, 1913.)

The number of glochidia on a single fish is remarkable, some 3,700 being found on one, well encysted and giving evidence of maturing on the host.   This, together with the relatively large number of infected fish taken, seems to fix this species as the natural host of the niggerhead.

The cases of infection observed on the black bass and crappies are probably either accidental infections which would not mature or they are the very similar glochidia of the pig-toe, *Q. trigona*, or the much less common *Q. solida*.   In these three species the glochidia are so much alike that they can not easily be distinguished when embedded in the tissues of the host, especially when their number is limited. The implantation upon this fish may be at any point on the gill filaments, but shows a tendency to distribution on the tips.   The filaments are so small that several are involved in a cyst, which is usually large for the size of the glochidium, as observed in artificial infections with this glochidium on other species of fish.   (See artificial infection, p. 20.)

Several glochidia occur in a common or compound cyst where they happen to attach closely.   A peculiarity observable in many preparations is the presence of spaces in the cysts apparently once occupied by a glochidium.   Adjacent to or near these may be glochidia. Surber (1913) has interpreted these as cases of migration of the glochidia.   This, if the correct interpretation, is a condition not previously observed.   I am not yet convinced that there is any migration except that necessary in escaping from the cysts, as examples may be seen where the glochidium has a well-defined sheath in what I understand Surber would consider the second position.

Infections on the blue herring during the remaining season were found most abundant in August, falling off in number in September, the latest being September 24 to 26, when 2 out of 9 were found infected.   My latest record for gravid niggerheads is September 3, 3 gravid out of 63 examined.   The difference of 23 days between September 3, the last record for the gravid mussel, and the 26th, the last for infected fish, as a rough indication of length of the parasitic period, would signify that in this case it is longer than in the case of the warty-back, *Q. pustulosa*.

Reference to a specimen of this fish taken on June 18, 1910, by H. W. Clark, revealed natural infection with the niggerhead.   This is the earliest season date that I know for an infection, but corresponds with our records of 5 gravid mussels on May 31 and 13 on June 17.

In the carrying of mussels by the herring we have an interesting example of a fish reported from salt water and possibly anadromous acting as a host for fresh-water mussels. In this case it seems probable that the mussels are attached during the stay only of the fish in fresh water; however, it supports the opinion of Simpson (1899, p. 282) that the presence of fresh-water mussels of the same species in parallel coastal streams can be explained by their being distributed by fish which are free to pass from the mouth of one river in the ocean to the mouth of another. (See also White, 1905.)

The blue herring seems not commonly to have any commercial use, at least in this region, though it has been reported as being used for food in the South. Although it has no recognized commercial value in the North, its really great value becomes apparent as the host of the most sought-after fresh-water shell. I have found the herring infected by another species of mussel, which observation is of interest as it shows that this fish is not the individual host of the niggerhead. The range of the herring is reported (Jordan and Gilbert, 1882, p. 266) as the Gulf of Mexico and the Mississippi Valley, abundant and resident in all the larger streams and introduced through the canals into Lake Erie and Lake Michigan. Twenty-six years later, Forbes and Richardson (1908) report it not common in Illinois. As the fishermen on the Mississippi in this vicinity do not seem familiar with it and make rather few catches, and there are reports of its having been abundant, it looks as if the fish were much less common at this point than formerly. There is this consideration, however, which would account for its escaping attention: It is a gamey fish requiring special means for its capture, and not being sought after, it may be more common than is apparent. The distribution of the fish corresponds with that of the mussel and it would be interesting to find any extension of the range of the niggerhead through the reported access of *Pomolobus chrysochloris* to the waters of Lake Erie and Lake Michigan. It may be, however, that the niggerhead, because of its natural habitat in swiftly flowing streams, could not thrive under lake conditions.

Artificial infection.—Artificial infection was not undertaken until a systematic search had been made for the natural host. Up until the middle of August, as I have shown in the discussion of the natural host, the only evidence secured was the finding of four infections on the following species: Black bass, *Micropterus salmoides;* black crappie, *Pomoxis sparoides;* white crappie, *Pomoxis annularis.* There were only one to four glochidia in each infection, therefore they were not as conclusive as could be desired.

As experiments with the niggerhead had been tried by other workers upon these species of fish without success, I went to work on the assumption that success had not been attained in these cases because

of unsuitable conditions in artificial infection. Some indication that this was the case was soon obtained. The glochidia would attach in some instances and not in others. It is of course necessary to imitate natural conditions as closely as possible as to temperature, aeration, light, etc. The results were more favorable when the sun was out than during cool, cloudy weather and apparently better in sunlight than in shade. It was found important to infect as soon as possible the same day after securing the gravid mussels, as this species will abort glochidia soon after capture. The cause is supposed to be that the lack of aeration due to confinement causes the animals to expel the glochidia which must tend to interfere with respiration. The small degree of special differentiation required to form a marsupium and the presence of the glochidia in all four gills of the *Quadrulas* undoubtedly contribute to this.

Infection and encystment of the glochidia were obtained. (Pl. III, fig. 24.) The latter was even observed under the microscope upon filaments severed from the gill and immersed in physiological salt solution. In one case observed the glochidium was completely covered by the encystment in four hours.

In the case of the fish left in tanks and aquaria the glochidia, although well encysted, were shed in from one to three days in all cases. The longest retention was found in the black bass. The cysts in these infections were exceedingly large, the excessive hypertrophy apparently being due to excessive stimulation. (See fig. 24.)

In one instance the fish were immersed in a salt bath (NaCl, 10 per cent) before introducing them to the container holding the glochidia. This resulted in more certain and rapid infection than usual in all species experimented upon, but the infection was no more persistent. The significance of the results in this experiment I will take up in the general discussion.

After the completion of a number of such experiments the discovery was made, as previously mentioned, of infections in large numbers on the blue herring, indicating it as the host fish for the niggerhead. This gave an explanation of the inconclusive results already attained, but, on the other hand, it did not offer ready means for the application of artificial infection. The host in this case is a fish which offers great difficulties to the methods at present employed in artificial propagation, in that it is rarely taken here and is difficult to retain in a living condition long enough to successfully subject it to infection. In order to find how to do this, it will probably be necessary to experiment in localities where both the fish and mussel are abundant. If possible to capture in pound nets or traps or by careful handling when seined, they could be infected without removal from the water. As the mussel is a species found in the larger rivers, inclosures would have to be made in a body of water having a current.

Since the fish is very active, suitable nets must be used to prevent injury. Trammel or gill nets, or seines of unsuitable mesh, would be fatal.

A satisfactory completion of the investigation of the parasitic stage in *Q. ebena* will probably be greatly aided by gaining more thorough knowledge of the fish's habits. This information will, of course, aid also in determining suitable measures for insuring the increase of the mussel.

Since some mussels, as the mucket, *Lampsilis ligamentina,* have been successfully carried through on more than one species of fish, the possibility of finding some more practical host in this case has been kept in mind. I am of the opinion that the experiments already conducted have been sufficiently thorough to demonstrate that the species so far tried are unsuitable. Chances for success would be looked for in closely related species. The only really common species in this locality answering these requirements is the gizzard shad, *Dorosoma cepedianum* (*Le Sueur*). Unfortunately this fish, like *Pomolobus,* is not readily kept alive; but the difficulties may not be insuperable. I have seen it kept alive several hours in the laboratory during the winter and have no doubt it could be kept in ponds, as it is found alive in bayous isolated from the river. As it has not yet, however, been found to carry mussels upon the gills, the probabilities of success are quite uncertain.

Three species of shad are found in the Mississippi. These are more closely related to *Pomolobus,* but they are not reported common north of St. Louis. Surber (1913) suggests the interesting experiment of infecting the species of herring to be found in the rivers of the Atlantic coast. This might be successful if tried in rivers containing considerable lime in solution, as is the case in the rivers in which the niggerhead thrives.

Propagation.—There is probably no shell for which there is a larger demand at present and its uses might be greatly increased. From the results already attained in the investigation of the life history of the niggerhead, propagation might be undertaken at once, provided it were done in a way that would permit of definitely ascertaining results. Whether the herring can be caught in sufficient numbers to make such operations practicable is a question, but reports would indicate that they can be in some localities. However, operations upon a large scale are hardly to be recommended before a demonstration of artificial infection and the completion of the parasitic period has been observed.

The remarkably full infection of this species in nature indicate that under natural conditions propagation of this mussel will take care of itself. Thus recommendations of measures for preventing the depletion of the niggerhead would be along the line of protection to the

herring as the host fish.   The cause for the increasing scarcity of the
herring seems not to be due to capture in large numbers, as the fish
is not commonly used for food throughout its range.   It is more
probable that it is due to artificial conditions, such as the obstruction
of its natural migrations by dams and the introduction into the
rivers of nonoxygenated sewage and the injurious wastes of manu-
facturing plants and the like.

Quadrula solida (Lea).   [Pl. vi, fig. 46, 47.]

Quadrula solida closely resembles *Q. ebena*.   I have investigated
this species only so far as to make some observations upon its breed-
ing.   I found gravid females May 31 and July 23.   In one specimen
glochidia were present in both inner and outer gills; in the other
cases only the outer gills were charged.   Glochidia were found mature
on both the dates mentioned.   The glochidium (pl. v, fig. 34) has
the subsemicircular form slightly more rounded than *Q. ebena*.

Dimensions: Height, 0.145 mm. to 0.16 mm.; length, 0.155 mm,
to 0.160 mm.   See also Surber (1912), to whom the material was
referred for description.   I have found no natural infections that
could with certainty be ascribed to this species.   Mr. Surber reported
a single glochidium on a *Pomolobus* infected with many of *Q. ebena*.
It would not be surprising if they are found to have the same fish for
host.

THE PIG-TOE, *Quadrula trigona* (Lea).   [Pl. i, fig. 10, 11.]

The brilliant orange-colored flesh of the pig-toe is characteristic,
although occasionally it is found yellow or white.   The nacre is a
beautiful silvery white, more or less iridescent; rarely the nacre is
pink.   In the manufacture of buttons it is less desirable than the
niggerhead because of less uniform thickness.

Habitat.—In the larger rivers, on a muddy bottom in rather deep
water.

Distribution.—Western New York to Minnesota, and Iowa, and
Kansas to Texas, east to Mississippi and Tennessee.   (Call, from
Baker, 1898.)

Juvenile.—The juveniles were the second most abundant of the 27
species I have collected and first in abundance among the *Quadrulas*.
They were taken on both mud and sand bottoms.   I have found this
species in the artificial ponds at Fairport, Iowa, introduced in the
parasitic stage on fishes—the second of the river-inhabiting *Quadrulas*
to be found under such conditions.

Glochidium (pl. v, fig. 33).—The breeding records of the Fairport
biological station for the past three years give June, July, and August
as months in which the glochidia of this species have been taken.   I
found seven mussels with early embryos of this species August 27 and
28, 1913, and one with mature glochidia on September 10, thus ex-

tending the known breeding period well on into September. In July I took a gravid example only 30 mm. in length; this surprisingly small size for breeding indicates the early attainment of the adult stage. The glochidial shell of this species seems thin and more delicate than in *Q. ebena*. The eggs are a pinkish red, the glochidia colorless, filling moderately all four gills. Unfertilized eggs were found with glochidia, so that gravid mussels have gills varying in color from a deep to a light shade, according to the number of eggs remaining undeveloped. The number of undeveloped eggs is surprisingly high, sometimes more than 75 per cent. The form of the glochidium is of the subsemicircular type (fig. 33).

Dimensions: Height, 0.136 mm. to 0.149 mm.; length, 0.136 mm. to 0.153 mm. The smaller size and straighter lines of the anterior and posterior edges of the shell should distinguish this glochidium from the similar glochidia of *Q. ebena* and *Q. solida*.

Natural infection.—The natural host for *Q. trigona* has not to my knowledge been determined with any satisfactory degree of certainty. I secured infections on *Pomoxis sparoides* August 2 and *Pomoxis annularis* August 9, observing in the first 2 and the second 4 glochidia which answer to the dimensions of *Q. trigona;* but as unmistakable preparations of these were not obtained it is not at present possible to state whether they may not be either *Quadrula solida* or *Q. ebena*. Since the host-fish for the latter has been pretty definitely determined to be *Pomolobus*, it might be excluded as a possibility here if it were not known that accidental and sporadic infections are possible on other than the usual host. A single case is reported as *Q. trigona* on the black crappie, *P. Sparoides*, by Surber (1913); he also reports an infection upon *Pomoxis annularis*, but thinks both of these may be accidental infections. Some evidence as to the natural host was obtained in the finding of the juvenile of this species in an artificial pond in which sunfish, crappie, and gizzard shad, *Dorosoma cepedianum*, had been kept. Since gizzard shad have not been found with gill infections, the evidence favors the sunfish and crappie in this instance. Further evidence was obtained in the successful implantation of the glochidia on the gills of the sunfish in artificial infection; this will be taken up in the next topic.

The character of the distribution of the juveniles of *Q. trigona* must be of some significance; it was found to be the most generally distributed of all species in explorations of the river bottom, from which it is a safe presumption that the host must be a common fish. To summarize the results, the evidence, though not conclusive, points to the sunfish and crappie as the hosts.

Artificial infection.—In my experiments with this mussel five species of fish were tested, *Micropterus salmoides, Lepomis pallidus, Eupomotis gibbosus, Pomoxis sparoides*, and *P. annularis*. Examina-

tion the second day showed many glochidia encysted upon the gills of the sunfish, but only one or two on the bass and crappie. The third day they were still in good condition on the sunfish, but all gone on the others. By the seventh day all were shed by the sunfish. Whether the parasitic period in this instance was completed I unfortunately did not succeed in determining. If it were, the period is a brief one and needs further testing. Experiments were conducted by T. Surber with this mussel at the Fairport biological station in 1910. The following fishes were used: *Micropterus salmoides*, *Pomoxis annularis*, *Aplodinotus grunniens*, and *Lepomis* (sp. ?). No implantation at any point on or in the body was observed, but free (without encystment) glochidia were found in the intestine of *A. grunniens* $17\frac{1}{2}$ hours after exposure. The results of my experiments point to gill infection as the normal method for this mussel and to good chances for success with *Lepomis pallidus*.

Propagation.—Propagation of this valuable mussel at present would probably have to be restricted to the introduction of the adult mussel in new territory. The success of this method can not be predicted with any degree of certainty until we know whether the host (presumably a fish) is found in the waters where introduction is attempted. A recent report of Wilson and Danglade (1912) recommends the introduction of this mussel into the rivers of Minnesota. Very practical work can undoubtedly be done along the line of extension of range of valuable species, but it would be obviously impractical to do this without a more certain knowledge than we have at present of the life history of this species. Take for example the case of the niggerhead mussel. So far as is known, it is dependent entirely upon the herring (*Pomolobus chrysochloris*) for propagation. Introduction into waters where this fish was absent would accordingly be certain of failure, as the mussels would be nonperpetuating. I have mentioned above the finding of many unfertilized eggs in the marsupia of these mussels. In the examination of hundreds of shells from various points in the region investigated I have found this state of things quite general. The result is that glochidia are difficult to obtain except in small numbers; under these circumstances artificial propagation would be quite impracticable.

THE BLUE-POINT, *Quadrula plicata* (Say). [Pl. II, fig. 17, 18.]

This form also bears the name of "three-ridge." It is at present one of the most-used shells in button manufacture.

Distribution.—Western New York to Arkansas and Iowa, Michigan to Alabama and Texas.

Habitat.—In the larger rivers, in rather deep water, generally on a muddy bottom (Baker, 1898).

Juvenile.—I have found this species with several others in the artificial ponds at the Fairport biological station. They have been

introduced, for the most part, probably in the parasitic stage on fish retained in the ponds. As the first example of the *Quadrula* group raised in captivity, it has interest and is something of a demonstration that they may be raised under such conditions. This was the fourth most abundant species in my collections from the river.[a]

Glochidium (pl. v, fig. 32).—The breeding records indicate that mature glochidia are to be found during June, July, and August. On June 26 I observed the spawning of this species. The mussel was marooned on a sand bar and only partly in the water, and the loose white mass of glochidia were collecting in a depression in the sand behind it. I suspect this was not perfectly normal spawning, since the mussel was being left by the receding water, and cases of abortion of glochidia are commonly observed in the *Quadrulas* when placed under conditions unfavorable for oxygenation in the gills. The glochidium (pl. v, fig. 32) is of the hookless type, subsemicircular, elongate, and white in color. It possesses a thread gland and larval thread like *Q. heros*, and probably the same will be found in all the other members of the Crenodonta group as limited by Simpson (1900). The gland is somewhat different in appearance from that in *Q. heros*. The turns or loops of the spiral are of about the same number, but a small portion of what may be designated the distal end, becomes abruptly two to three times broader than the remainder. This larger portion begins at the posterior end of the hinge line and on reaching the anterior side of the adductor muscle curves in close to its ventral and posterior side. The contents of this enlarged portion is the coiled hyaline thread secreted by the gland, in a less condensed state than at the time of its emergence from the external pore, which lies on the posterior side of the adductor muscle.

The dimensions of the glochidium are: Height, 0.195 mm. to 0.215 mm.; length, 0.185 mm. to 0.200 mm.

Natural infection.—Five examples of natural infection with this species were obtained during June, July, and August. The fish were all crappies, both *Pomoxis annularis* and *sparoides* and were caught chiefly in the channel of the Mississippi on or near mussel beds where *Q. plicata* was abundant. Surber (1913) reports two cases, one on *S. canadense* and one on *P. annularis*, both for July 20. In determining natural infection of this species it is necessary to distinguish it from the glochidium of the "spike" mussel, *Unio gibbosus* (Barnes), as the latter has a similar form and dimensions, and it apparently infects some of the same species of fish. Typical glochidia differ in the following respects:

The dimensions in *U. gibbosus* are: Height, 0.208 mm. to 0.220 mm.; length, 0.190 mm. to 0.208 mm. The hinge line is proportionately

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[a] I have received two juveniles of this species about 5 mm. in length, possessing a well-defined byssus. This material was collected in Lake Peppin by Mr. A. F. Shira.

longer and the thread gland curves in from the ventral edge of the right valve in *U. gibbosus.* In *Q. plicata* the ventral loops follow a peripheral course (see fig. 32). Unfortunately, this character is difficult to distinguish in glochidia which are imbedded in the tissues of a fish. Again, since the gland is an embryonic organ, it does not persist long after metamorphosis commences in tissues of the host. In natural infections it is not always possible to obtain an orientation of the specimens so as to obtain the most accurate measurements; especially is this the case when a fish carries only one or a few glochidia, when distinction between glochidia is made more difficult.

The number of infections determined as *U. gibbosus* were as follows: Black and white crappies, 5; yellow cat (*Leptops olivaris*), 1; Sauger (*Stizostedion canadense*), 1. In addition to these, I have records of three infections on the black bass (*Micropterus salmoides*) which belong to one of these species but which I am at present obliged to consider as doubtful.

Summarizing the results, the chief hosts for *Q. plicata* are indicated as the crappie, *Pomoxis annularis* and *Pomoxis sparoides*, with the sauger and black bass as occasional possible hosts. The reported (Lefevre and Curtis, 1912) successful artificial infection of *Micropterus salmoides* with *Q. plicata* would warrant the expectation of finding this fish infected in nature.

The presence of an embryonic thread suggests the possibility of fin infection from analogy with forms that possess that organ. The small size of the glochidium and lack of color would make them more difficult to detect than the fin-infecting glochidia of the *Anodontas.*

Artificial infection.—The artificial infection with this species which I have just mentioned as having been made by Lefevre and Curtis (1912) was the first reported and the only successful infection with *Quadrula* mussels so far as known to me. The fish, black bass, *Micropterus salmoides*, were infected August 5, 1908, exposed 30 minutes to infection, and young mussels liberated on August 17, giving a parasitic period of 12 days in water of 24.4° C. average temperature.

I have experimentally infected the following fish with this species: White crappie, *Pomoxis annularis;* black crappie, *P. sparoides;* yellow perch, *Perca flavescens;* sunfish, *Lepomis pallidus;* bullhead, *Ameiurus;* flathead catfish, *Leptops olivaris;* channel cat, *Ictalurus punctatus;* quillback, *Carpiodes velifer.* The first four named proved suitable as carriers of this species; the young mussels were carried through the metamorphosis in large numbers, and I was able to secure specimens of the young juveniles alive on the bottom of the aquaria in which the fish were retained. In the sunfish a large number were apparently shed prematurely, while a few were carried through to maturity. The bullheads carried a few for the full time, but on the

fins and not the gills.   The remaining species shed the glochidia in from one to two days.

In the successful cases the period of parasitism varied from 8 to 11 days, the water temperature averaging approximately 76° F.   The last to mature seemed to be at the tips of the filaments, thus indicating that the position was an important factor in determining the parasitic period.   The young mussels on leaving the fish show no appreciable development of shell; thus they are very minute at this stage and probably a prey to many enemies.[a]

Propagation.—Several factors favor the artificial propagation of this species upon a practical scale.   It is common and at present one of the most used shells in the button industry.   It seems to be a form not narrowly restricted as to hosts and these are indicated to be among the commonest and most readily obtainable fishes. Although a river form, its habit as a dweller in stiller water and on a mud bottom makes it susceptible to propagation or control under conditions readily imitable in artificial lakes or ponds.   A continuous water supply is desirable; my observation has been, however, that it will survive rather adverse conditions in this respect.   I have collected many live specimens from a slough which had gone dry to the extent that only mud remained.   Under these conditions the majority of the pond mussels, *Anodonta   corpulenta*, had died.   I would cite also the finding of this species accidentally introduced in the parasitic stage into an artificial pond at Fairport, Iowa.   The pond had gone dry and I found a specimen still alive buried in mud barely moist.   It is evident, I think, from these observations that the species is hardy, at least as regards some of the more common vicissitudes to which mussels are naturally subjected.

THE WASHBOARD, *Quadrula heros* Say.   [Pl. II, fig. 14, 15.]

This is the largest and one of the most handsome of American fresh-water mussels.   Its unusual size adapts it to special uses, and in some localities it has the reputation of being one of the best of pearl-bearing species.

Distribution.—Mississippi River system generally; Red River of the North; Tombigbee River, Ala.; southwest to Nuevo Leon, Mexico (Simpson, 1900).

Habitat.—It is found in large rivers in deep water and on muddy bottoms.

Juvenile (pl. II, fig. 13).—The juveniles are very handsome because of their elaborate shell sculpture.   They were taken in the same locations as the adult, viz, in deep water on a mud bottom.

Glochidium (pl. v, fig. 35).—I obtained mature glochidia of *Q. heros* September 24, having taken early embryos August 24 and immature glochidia as early as August 28.   During October, in

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a See p. 12, footnote, regarding observations of the destruction of young *Q. pustulosa.*

observations covering two successive seasons, the mature glochidia were readily obtained, as the majority of adult females examined were gravid.   An examination on November 7 of 55 individuals from the same mussel bed yielded no gravid specimens at all, and some 50 mussels in March and April yielded 1 gravid specimen only; this was found April 14, and contained immature glochidia, still surrounded by the vitelline membrane.   All the information available indicates that the regular breeding season is during the autumn, chiefly October, with an extension into the winter months in some localities, but that the glochidia are not carried a long period in the gills as in the Lampsilinæ.   Since all four gills are used as marsupia and greatly distended, a long breeding period would seem to be too great an interference with the breathing function of the gill.

The productivity of this form is enormous, a single average-sized individual in which I estimated the number gave one and a third million young.   A count was made of a definite fraction of a marsupial chamber in a gill and the total computed from a count of these chambers for the four gills, account being taken of difference in size in the gills.   Simpson (1899) quotes Lea as giving the number of young produced as 6,000,000.   I have not seen the original of this statement by Lea, but find another (Lea, 1857, p. 40) in which he gives an estimate of 3,000,000 or 4,000,000 as the number produced; as he says "probably to the number of 3,000,000 or 4,000,000," he may not have made an actual computation.   A specimen twice the size of the one I considered, which would be unusually large, would hardly have more than 3,000,000.   From this I suspect that Lea's estimate is too high.   Lefevre and Curtis (1912, p. 144) say in regard to the breeding period of this species that, finding young embryos in May, their observations are not in accord with those of Frierson (1904), who found glochidia in January and so concludes that *heros* is an exception to the genus *Quadrula* and not a summer breeder. Conner (1909) gives an observation of breeding in November.   Surber (1912) figures an immature glochidium, giving dimensions which correspond closely with the mature embryo, together with observations on the breeding season.   Simpson (1900, p. 776) is of the opinion, since he has seen so few gravid specimens, that the breeding of these species is only at long intervals.   It is apparent from the above references that the observations upon the breeding of this species have been quite limited and I know of no description of mature glochidia, with the exception of Lea's (1857, p. 46).   In his description there is no reference to the time of breeding and he has omitted anatomical features that are distinctive.   He says:

Unio multiplicatus (synonym for *Q. heros*) Lea, figure 3.   Pouch shape; dorsal line long; side margins gently curved, basal margin slightly rounded; color clear white. Has no hooks.

The above is sufficiently accurate as to the features described but is not enough to identify the glochidium, since there are so many forms answering this description. I think the following will serve to distinguish it:

Dimensions: Height, 0.316 mm. to 0.340 mm.; length, 0.250 mm. to 0.260 mm. The right valve contains a large and conspicuous thread gland; this is in the form of a spiral rod (pl. 3, fig. 21) tapering at each end, and having about two turns about the adductor muscle. As compared with this gland in *Anodontas*, it is more conspicuous because of its greater width and its being possibly more highly refractive to light. The inconspicuous tapered extremities lie near the ventral side of the adductor muscle and one of them opens to the mantle cavity; from this opening the larval thread extends. The latter is of considerable length and lies coiled in the mantle chamber. It consists of a delicate hyaline thread which becomes readily extended when the glochidia are extruded from the parent gills. The presence of a thread gland has not been previously reported for the *Quadrula* group, I believe, and only in the *Anodontas* and the *Unios* (as listed by Ortmann, 1912). I find it present in *Pleurobema æsopa* and also in *Unio gibbosus*, for which, with the closely related forms, Ortmann has created the new genus *Elliptio*.

Natural infection.—When the investigation of the breeding of this mussel was undertaken very few data were available; in fact, the published accounts, as I have shown, indicated considerable uncertainty about the breeding period. I was fortunate in finding gravid mussels with active glochidia in considerable abundance and suitable for experimentation. This situation led me to accept the opportunity presented before I was able to investigate sufficiently the problem as to the natural host. I subjected a number of species of fish to infection, obtaining quite definite results. The following species carried the glochidia successfully on the gills or the fins: The sunfish, *Lepomis pallidus* (pl. IV, fig. 26b); the catfishes, *Ictalurus punctatus* and *Ameiurus melas;* and the drum, *Aplodinotus grunniens.* Some months after these experiments were made Mr. T. Surber, in examination of Arkansas fishes taken in January, reported several natural infections by this species on the fins of a sheepshead, *Aplodinotus grunniens*, but none on the gills. More recently I have had the opportunity of examining a number of fish taken in the Mississippi at three different stations. Among these I found infected by the larva of *Q. heros* five species of fish and the batrachian, *Necturus maculosus*. These observations are shown in detail in table 2.

The infections upon *Necturus* were none of them encysted, even after attachment for a known period of several days, which leads me to believe that the mussel is incapable of development upon this host.[a]

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[a] Incidentally the observation may be of interest of a larval mussel of another species abundant upon *Necturus* completely encysted and passing through its metamorphosis on this animal.

TABLE 2.—NATURAL HOST OF FRESH-WATER MUSSEL QUADRULA HEROS.

Name of host.	Date.	Locality.	Number of glochidia.		Development.
			Gill.	Fin.	
Necturus maculosus	Oct. 20	Moline, Ill	Few.	......	Not encysted.
Do	...do	...do	Few.	......	Do.
Do	Oct. 22	...do	Few.	......	Do.
Dorosoma cepedianum	...do	...do	......	25	Do.
Pomoxis annularis	...do	...do	......	22	Do.
Dorosoma cepedianum	Oct. 24	...do	......	48	Completely encysted.
Do	...do	...do	......	17	Do.
Do	...do	...do	......	2	Do.
Pomoxis annularis	...do	...do	......	1	Undetermined.
Do	...do	...do	......	1	Do.
Roccus chrysops	Oct. 25	Fairport, Iowa	3	......	Encysted.
Amia calva	Oct. 28	Moline, Ill	1	......	Do.
Necturus maculosus	...do	...do	Many.	......	Not encysted.
Leptops olivaris	Nov. 7	Hampton, Ill	2	......	Deeply encysted.

The results of the artificial infection experiments and the observations upon natural infections would indicate that this mussel may carry out its development upon both the gills and fins of a number of species of fish. In the natural infections it will be noted that the infection of the fins was more common.

This is an interesting case of a hookless glochidium adopting partially the fin-infection habit which is found in the *Anodontas*. It has other characters in common with this group in the large size of the glochidium, in the presence of the large thread gland, and in the winter (though probably not long period or bradytictic) breeding habit. The opinion of Simpson (1900, p. 766, footnotes) that this species breeds only at long intervals was based upon the absence of observations of gravid specimens. I think this scarcity of records may be ascribed partly to the following causes: The breeding season is at the time of year when less collecting is being carried on, as well as at a different season from that of related forms. Again, gravid mussels abort the glochidia so that the evidence is liable to be lost unless observed when the mussels are first removed from the water. I think the assumption that they breed annually is safe until more definite evidence to the contrary is found.

Artificial infection.—Mature glochidia suitable for infection were first obtained September 24, and subsequently other gravid mussels were obtained, apparently being not difficult to find. It was noticed that the glochidia had unusual vitality, it being possible to use the same lot day after day for more than a week. This is in marked contrast to the conditions I have encountered among other *Quadrulas*. It is possible that it may be associated with the lower temperatures at this season. Another feature of importance is the immense number of glochidia, which increases greatly the ease of manipulations.

Some 10 species of fish were subjected to infection in six different lots, according to the usual method. The results of these experiments are summarized in table 3.

TABLE 3.—ARTIFICIAL INFECTION OF QUADRULA HEROS SAY.

Date.	Exper-iments.	Fish.	No. of fish.	Glochid-ium re-tained until—	Period on fish.	En-cysted.	Position.
Sept. 25	30–34	P. annularis......	7	Sept. 26	1 day.........................	No....	Gill.
25	30–34	P. sparoides......	9	Oct. 1	6 days........................	Yes...	Do.
Oct. 1	30–34	R. chrysops.......	4	Oct. 6	5 days........................	Yes...	Do.
Sept. 27	30–34	M. salmoides.....	4	Oct. 8	11 days.....................	Yes...	Do.
27	30–32	I. punctatus......	7	Feb. 7	4 months 11 days a..........	Yes...	Fin.
27	30–35	A. melas..........	2	Feb. 11	4 months 15 days a..........	Yes...	Gill and fin.
27	30–35	L. pallidus	8	{Dec. 6 {Feb. 5	}2 months 9 days to 4 months } 9 days.	}Yes...	Gill.
25	30–35	S. canadense......	5	Oct. 5	10 days......................	Yes...	Do.
Oct. 25 / 7 / 1	} 30–35 / 34	A. grunniens ..... C. difformis.......	6 1	Apr. 18 (Died.)	6 months 11 days a..........	Yes... Yes...	Fin. Do.

a Glochidia remained upon the fish after the date observed.

It will be noted that both gill and fin infection persisted more than four months on the catfishes, *Ictalurus punctatus* and *Ameiurus melas;* gill infections remained upon the sunfish over two months (pl. IV, fig. 26b). In these cases evidence of development was found, but not determined for the shorter periods of 11 days or less. In *Aplodinotus,* fin infections remained till April, more than six months, and showed considerable development at the time of examination.

The indications are that infection takes place chiefly during the autumn, possibly to some extent in winter and early spring, and that the young mussel leaves the host when the water becomes warmer in the later spring. The readiness with which the glochidia become attached to fish in the autumn would indicate that this is a natural time for infection, although for some long-period breeders (*Anodonta*) it is claimed that development proceeds during the winter before leaving the parent gill (Lillie, 1895). Lillie states that the glochidia are carried through the winter and are extruded finally in the spring; the species to which he refers is *Anodonta cataracta.* Lefevre and Curtis say that *Anodontas* have mature glochidia early in October. An experiment performed at the Fairport laboratory by Messrs. Clark and Surber September 26, 1910, with *A. corpulenta* resulted in attachment of glochidia upon fish, but temporarily only. From these citations it would seem that there is difference of obser-vation as to the maturity of glochidia in the genus *Anodonta.* There may be a considerable difference as to date of maturity for different species of the genus, as is the case in the genus *Quadrula.*

The difference in duration of the period of attachment to fishes in the different hosts is to be noted. I am not at all certain of the explanation. If, as reported by Schierholz (1888) and Harms (1907–1909), the duration of the parasitic period varies inversely as the temperature of the water, that would not explain the liberation of glochidia from sunfish in midwinter. One must assume a difference of rate for different hosts or that development was incomplete in the case of the shorter periods.

The possibility of implantation upon both gills and fins of the host seems to be more liable to occur in this species than in any other of which I know having hookless glochidia. This habit might naturally be correlated with the large size, which would enable the glochidium to become attached more readily to the exterior of a fish, where places for attachment are coarser than on the gills. This character should be of advantage in artificial infection, through more diffuse distribution on the fish and on less vital parts, permitting a higher optimum infection. In the present experiments the largest number of glochidia carried through four months was 28;[a] this, however, should not be considered any criterion of possibilities, since the parasitic period in this case is probably an unusually long one. In general for the long-period breeders it is probably more economical, other things being equal, to infect in the spring, thus securing a shorter and more certain development.

The infection of the fins in the catfish calls attention to a difference in suitability to infection between such a fleshy fin and the membraneous type of the Centrarchidæ, which group has been found so favorable for gill infections.

The encystment of the glochidia of *Q. heros* (see pl. IV, fig. 26b) indicates a less vigorous reaction of the hosts tissues than, for example, in the niggerhead; in that the cysts are comparatively thin.

Propagation.—The very large size of *Q. heros* and the thickness of the shell give possibilities of use which are found in no other mussel. At the present time it is, according to manufacturers, with the mucket, *L. ligamentina*, and the three-ridge, *Q. plicata*, one of the three chief shells used in the button industry, possibly taking first place for large buttons; in quality it is considered second grade, but varies with locality. From the results of this investigation it is shown to be one of the most favorable among the *Quadrulas* for artificial propagation. The reasons for this are as follows: It is a fall or winter breeder, thus not being limited to a brief summer breeding period at a season when it is more difficult to deal with live fish and at a time when the other *Quadrulas* are breeding. It has at least three host fish and probably more upon which it can be propagated. The tremendous number of glochidia produced and their great vitality are features that increase the chances of success in artificial propagation. Its natural habitat is more easily imitated under artificial conditions than that of species which are restricted to river channels in that it is found in the more quiet waters of lagoons and lakes as well as in the open rivers. For a heavy shell it is a rapidly growing species.

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[a] Through the winter of 1913–14 *Q. heros* was carried to maturity in large numbers (800 to 1,200 per fish) on the gills of the following: *Pomoxis annularis*, *P. sparoides*, *Lepomis pallidus*, *Apomotis cyanellus* and *Ameiurus* Sp., and in smaller numbers on the fins of the following: *A. grunniens*, *Ictalurus punctatus*, *Ameiurus* Sp.

Natural hosts of mussels of Quadrula group.—Natural infections of fish by mussels of the *Quadrula* group were found as follows, the figures representing the number of fish:

Warty-back (*Q. pustulosa*), on—
    Yellow catfish (*Leptops olivaris*), 1.
    Spotted catfish (*Ictalurus punctatus*), 9.
    Crappie (*P. annularis*), 1, reported by Surber, 1913.
Pimple-back (*Q. pustulata*), on—
    Crappie (*P. annularis*), 1, reported by Surber, 1913.
Monkey-face (*Q. metanevra*), on—
    Bluegill sunfish (*Lepomis pallidus*), 1; 5 reported by Surber, 1913.
    Blue sunfish (*Apomotis cyanellus*), 1, reported by Surber, 1913.
    Sauger (*S. canadense*), 1.
Niggerhead (*Q. ebena*), on—
    Large-mouth black bass (*M. salmoides*), 1(?).
    Skipjack (*Pomolobus chrysochloris*), 11, reported by Surber, 1913.
Q. solida, on—
    Bluegill sunfish (*L. pallidus*), 2, reported by Surber, 1913.
Pig-toe (*Q. trigona*), on—
    Pomoxis sp?, 1.
    Crappie (*P. annularis*), 1.
    Strawberry bass (*P. sparoides*), 1, 1(?) reported by Surber, 1913.
Blue-point (*Q. plicata*), on—
    Large-mouth black bass (*M. salmoides*), 3(?).
    Pomoxis sp.?, 2.
    Crappie (*P. annularis*), 2; 1 reported by Surber, 1913.
    Strawberry bass (*P. sparoides*), 1.
    Sauger (*S. canadense*), 1.
Washboard (*Q. heros*), on—
    Fresh-water drum (*A. grunniens*), 1, reported by Surber, 1913.
    Eel (*Anguilla chrysypa*), 1, reported by Surber, 1913.
    See also table 2.

TABLE 4.—COLLECTION OF JUVENILE QUADRULAS, SEASON OF 1912.

No. of station.	Name.	Date.	Dredge hauls.	Depth.	Bottom.	Q. pustulosa.	Q. pustulata.	Q. granifera.	Q. lachrymosa.	Q. metanevra.	Q. ebenus.	Q. solida.	Q. trigona.	Q. plicata.	Q. heros
1	Iowa Shute.......	June 20	9	3–6	Sand and gravel.	3	....	....	....	....	....	....	3	1	...
2	Smiths Cove to Pine Creek.	June 22	15	4–8	Varied(see hauls)	2	....	....	....	1	....	....	....	....	...
3	Sand bar above Smiths Creek.	June 25	0	....	Sand silt........	0	8	....	....	....	....	....	3	1	...
4	.....do............	{June 26, June 28}	0	0–1	.....do...........	0	2	....	....	....	....	....	3	2	...
5	Pine Creek........	July 10	4	2–8	1, mud; 2, 3, and 4, mud and gravel.	4	....	....	....	1	1	....	4	3	.--
6	Pine Creek to Buffalo.	July 12	11	2+	1–6 gravel; 7–11, mud and gravel.	5	1	2	...	1	1	...	17	15	...
7	Montpelier........	July 15	5	Varied.	Varied(see hauls)	1	....	1	...	....	....	...	2	....	...
8	Barrs Landing....	July 17	2	2–5	Gravel and mud.	11	....	....	1	2	....	....	16	6	...
9	Wagglers Landing	July 29	5	3–5	Gravel and sand.	12	....	1	...	8	....	....	7	5	a1
10	Moline............	Sept. 24	4	2–4	Sand and mud..	0	....	....	....	....	1	...	1	5	{1+ a3}
11	.....do............	Sept. 26	5	2–4	Mud............	1	1	....	....	....	1	...	3	10	...
12	Davis Point......	{Dec. 14, Dec. 23, Dec. 24}	0	½–4	Pebbles..........	0	....	....	....	....	....	...	....	....	...
						39	12	4	1	13	4	0	59	48	5

a Over 20 mm. and under 65 mm.

GENERAL DISCUSSION.

In the investigation of the specific problem of propagating the *Quadrulas* some results have been attained which are of general application probably to all the Unionidæ. Also observations have been made incidentally upon other species which, as they have a bearing on the present problem, require discussion.

REPRODUCTION AND EMBRYONIC STAGES.

As practical propagation of the Unionidæ is only indirectly concerned with the embryonic stages, I have not dealt with these in the body of this paper. My observations upon these stages have been very limited and incidental only to other studies, but as the *Quadrulas* have had little attention some of these may be worth mentioning. Reproduction among the *Quadrulas* seems to be essentially as reported in other Unionidæ (Rabl, 1876; Schierholz, 1888; Latter, 1891; Lillie, 1895). The sexes are separate so far as known. The gonads occupy a considerable portion of the visceral mass among the coils of the intestine. The eggs upon extrusion from the genital apertures pass into the suprabranchial chambers of the inner gills, passing from there to the cloaca and then back through the suprabranchial chambers to the gills. They are probably fertilized during transition to the gills by sperms introduced with the respiratory current. I have observed ovulation in *Quadrula ebena* and remarked the exceedingly fine stream of eggs issuing singly and covered by mucous envelope; the passage to the gills was not observed, but it would seem strange in these forms which carry embryos in all four gills that the eggs should not go directly into the inner gills, as they must pass the openings of the water tubes.

Contributions to a knowledge of the development from the eggs to the glochidial stage among Unionidæ have been made by Flemming (1875), Schierholz (1878, 1888), Goette (1891), and these stages have been completely described for *Unio complanata* and *Anodonta cataracta* by Lillie (1895).

While making examinations for breeding periods I was much astonished to note the slowness of division processes. The eggs of *Q. ebena* examined in the morning of May 31 seemed to be all in the one-celled stage; in the afternoon two-celled stages were present. The second day segmentation had advanced to the four- and eight-celled stages only, and the fourth day 16-celled stages predominated. Since making these observations I have read Lillie's (1895) paper and see that he has commented upon the phenomenally slow segmentation in the forms which he examined, *Unio complanata* and *Anodonta cataracta*, contrasting it with the rapid development in marine lamellibranchs.

PARASITISM.

There are questions associated with the parasitism of fresh-water mussels which have previously had little discussion. Obviously the basis for a consideration of these must be upon observation of natural infections. I wish to discuss these under the following heads: Restricted infection, susceptibility and immunity, frequency of infection, extent of individual infection, conditions of infection in nature, etc.

Restricted infection.—The existence of specific or narrowly restricted parasitism in the case of some mussels I believe I have demonstrated in the case of *Q. pustulosa* upon the channel cat, *Ictalurus punctatus* (Howard, 1912). A similar case is that of the niggerhead upon *Pomolobus chrysochloris* (Surber, 1913). These are not surprising, since it is common, especially among animals, for a certain species of parasite to be restricted to a given species or genus of hosts, as *Goniodes stylifer*, the louse infesting the turkey, and *Trichodectes scalaris* upon the ox. If by accident they come in contact with some other animal they do not remain. Why? The supposition is that the reaction of the blood or something about the foreign hosts is unfavorable to them; in anthropomorphic language, "they do not like it."

To what extent this principle of limited parasitism extends among mussels is still to be determined. It seems obvious, however, that a solution of this question is logically to be sought from a study of natural infections.

The method of determining the host by artificial infection has proved practicable in the experiments reported by Lefevre and Curtis (1912), but in these cases the mussels were parasitic upon common and easily obtainable fish. The chief commercial species employed was the mucket, *Lampsilis ligamentina*, and the fish successfully infected were the sunfish, *Apomotis cyanellus*, and the black bass, *Micropterus salmoides*. In the experiments at the Fairport biological laboratory black bass, sunfish, and crappies were infected successfully; the pike, *Esox lucius*, and the perch, *Perca flavescens*, were reported doubtful. From these results it would seem that infection with the mucket is limited chiefly to the Centrarchidæ, a single family of fishes. The hooked glochidia of *Anodonta corpulenta* seem less restricted. I have seen these upon fish of the following families: Clupeidæ, Centrarchidæ, and Sciænidæ. A similar state of things is seen in the hookless external infecting glochidia of *Q. heros* successfully maintaining itself on the Sciænidæ, Siluridæ, and Centrarchidæ (the latter two observed in artificial infection).

Susceptibility and immunity.—The commonness of infections on some species of fish in nature might be called a sign of susceptibility

in those species. The drum or sheepshead, *Aplodinotus grunniens*, is found infected commonly with the glochidia of *Lampsilis lævissima*, *L. gracilis*, *L. alata*, *Plagiola donaciformis*, and others. The drum is a mussel-eating fish (see Forbes and Richardson, 1908), so that we have an explanation of the presence of the larva of these thin-shelled and so readily eaten mussels upon its gills. In the above example we have several species of mussels parasitic upon one species of fish. From many examinations of the channel catfish, *Ictalurus punctatus*, I have found only one species of mussel, viz, *Q. pustulosa;* this seems to be the other extreme.

The failure to obtain gill infection with certain species has been mentioned (see introduction). I have observed a similar immunity in examinations for natural infections on the gills of the gar pike, *Lepidosteus platostomus*, the dogfish, *Amia calva* Linnæus, and the suckers, the Catostomidæ. Upon obtaining fuller data such cases may perhaps prove to have their parasitic species, at present unknown. It is to be noted that these reported cases of immunity refer to gill infection and that the absence of these possibly does not preclude infection of fins. We have not found infections on the gills of the gizzard shad, *Dorosoma cepedianum*, but Mr. A. F. Shira has found the fins of this species infected.[a]

Lefevre and Curtis, in seeking an explanation of immunity, raise the question as to whether the factors are chiefly mechanical or are an histological response of the fish's tissues. In my opinion both of these operate, and there is still another factor, viz, the failure of glochidia to fasten when the appropriate host is not found. The histological response begins with the hypertrophy resulting in the formation of the cyst; this occurs in most cases whether the parasite is retained or not. If not, the cyst is shed by a process of desquamation of the external epithelium. I have observed this in gill infections only. A stream of water of not great force will remove the outer layers of epithelium of an infected gill about to shed the glochidia. Such a catarrhal reaction is presumably the result of the irritation set up by the glochidium. The question arises as to what prevents such a reaction in cases of successful implantation. Is it merely absence of immunity in the host, or does the glochidium supply an active agent in the nature of an anæsthetic to prevent the irritation that would be expected? Mr. Thaddeus Surber once called my attention to an apparent case of acquired immunity in some sunfishes which received glochidia upon the first infection but not the second. This is a matter that should be investigated, as the existence of such a possibility would prevent the use of fish more than once successfully in artificial propagation.

[a] Since writing this, I have found infections by *Q heros* upon the fins of this species, also infections by other mussels upon the gills of the gar-pike and the dogfish. (See table 2.)

Some of the mechanical factors in immunity mentioned by Lefevre and Curtis were such as configuration of mouth parts, texture of gills, smallness of gill openings, and rapidity of fin movements. The third factor which I suggest, viz, failure of glochidia to react, was observed in experiments upon the niggerhead, *Q. ebena*, and the warty-back, *Q. pustulosa*. In the latter case the glochidia fastened readily upon the catfish, but not upon other species of fish upon which the glochidia of the mucket, *L. ligamentina*, will fasten readily. It is difficult to obtain any infection with the glochidia of the niggerhead upon the members of the Centrarchidæ; however, under certain circumstances (see the next topic) they will take hold so vigorously as to threaten overinfection. From such results it seems not improbable that the tissues or blood of the nonhost possess reactions in the nature of antibodies, precipitins, and other immunizing agents, such as those discovered in the higher vertebrates, while the glochidium is especially adapted to the reactions of the appropriate host.

Induced susceptibility.—I have already mentioned, in discussing the niggerhead, an experiment in which fish were immersed in a solution of common salt (10 per cent, by weight) before placing in the infecting tank, where it was shown that this treatment had the marked effect of causing rapid infection where previously it had been difficult to obtain. We have here possibly a suggestion that this reaction is related to the normal habit of the glochidium in responding to the presence of its natural host, the blue herring, a fish reported from salt water and possibly anadromous. However, one would assume that all perceptible traces of the more saline medium would be lost when the fish had passed through a few miles of fresh water. In my opinion, there is no causal connection here, since glochidia of many species show excitement in the presence of sodium chloride and other salts. This is due undoubtedly to the fact that their normal reaction is to chemical stimulation from the ions of protoplasmic salts diffused from the animal fluids of fishes' gills or bodies. As the glochidia did not remain upon the fish through the parasitic period, a probable explanation would be that the salt could have had only the effect of overcoming the inhibition of the glochidia to react.

The effects of the parasitism of the glochidium upon the host and the exact relations to the host at various stages in the developing mussel are matters the investigation of which should be productive of interesting results. Lefevre and Curtis (1912) record observations of the ingestion of portions of the host's tissues by the glochidium soon after implantation. It is a question whether the host continues to supply sustenance other than oxygen in forms like *Lampsilis ligamentina*, which show little or no increase in size. In forms like those of the *Proptera* (Ortmann) group, which increase to a considerable extent in the parasitic stage (see metamorphosis during the

parasitic stage), the host must furnish the material. In these cases I have observed ocular evidence of absorptive processes whose exact nature I hope to investigate later.

Frequency of infections.—To know the proportion of infected fish in nature is a matter of considerable importance. The expectation would be that it must, from the nature of the case, vary according to species, locality, season, abundance of mussels, source of the fish, and the like. The results I have given for the channel cat, *Ictalurus punctatus*, give an idea of the variation that occurs. We see that for this fish during the months of July and August, the breeding season for the warty-back *Q. pustulosa*, there were 17 infected fish out of 39 examined. The entire absence of infections in September from an examination of 98 fish is explained by the season, which was after the close of the breeding period for the mussel. The figures given by Surber (1913) of no infections out of 21 fish of this species examined in August, I can hardly explain unless it is that the fish were not taken near mussel beds, or that owing to the position of the glochidia they might be easily overlooked in living fish.

The drum or sheepshead, *Aplodinotus grunniens*, on account of the fact that it is the host for a large number of species, runs the chance of more frequent infections.

In a region where artificial infection has been carried on upon a large scale, it would be difficult to determine satisfactorily anything of this nature regarding the species employed in the operations; this difficulty has arisen in investigations at the Fairport biological laboratory, fish having several times been captured which had been without doubt artificially infected.

Extent of individual infections.—Certain species of fish commonly in nature carry a remarkably large number of glochidia; for example, the drum, *Aplodinotus grunniens*, and the herring, *Pomolobus chrysochloris*, have been found with thousands; but a small number seems more common. Heavy infections are difficult to explain, except upon the supposition that they take place at the time of extrusion from the mussel, or as the result of oft-repeated infections. This brings up the subject of the following topic.

Conditions of infection in nature.—I know of no observations of the infection of fish in nature. Latter (1891) found that he could produce a discharge of glochidia by gently striking the water in which anodons were lying and made further observations upon the emission of glochidia which, he seems to conclude, argue against the necessity of the presence of fish. I believe, however, they support the probability that the approach of fish is the normal stimulus in eliciting the emission of glochidia. The cases of heavy individual infection of fish found in the species mentioned above suggest that the glochidia must be extruded when the fish are in close proximity, otherwise the

glochidia would be too widely distributed to make heavy infection possible. We find the heaviest infections with glochidia of the niggerhead, which lives in swiftly flowing water. It would be quite reasonable to expect adaptations here comparable to those seen between insects and plants, not necessarily as elaborate as that between the rein-orchids *Habenaria* and fertilizing moths, but something of that nature would be equally advantageous to a species of mussel. The expected features in such a relation would be some attractive agent in the mussel, the perception by the latter of the fish's presence, and the reaction of extruding the glochidia. Mussel beds are known to offer attractions to fishes because of the associated life in their vicinity, such as worms, crustaceans, and the like. During the summer of 1912, Dr. W. P. Herrick called my attention to at least three instances of fish (sunfish in each case) being taken in his crates which contained live mussels. We have abundant evidence of attractions to some species of fish, e. g., catfish and sheepshead, in the food which the thin-shelled species of mussels supply (Forbes and Richardson, 1908, quoted above, and Kendall, 1910). This is a rather vicarious offering, and it is not known to be made by the heavier-shelled species among which we have found cases of narrowly restricted parasitism. It is among these that we would expect some special adaptations.

Type of infection.—In observations upon natural infections I have found that in general the hooked glochidia were to be found upon the fins and the hookless upon the gills, as has been reported by others, chiefly from artificial infection (Harms, 1909; Lefevre and Curtis, 1912). I find, however, there are some apparently constant exceptions. I have mentioned above the observations that the hookless glochidium of the washboard mussel, *Quadrula heros*, was found to be a fin-infecting species. Its considerable size apparently adapts it to this mode of infection. The presence of a larval thread also suggests a possible relation to this habit because of the presence of that organ in the fin-infecting hooked glochidia. In support of this is the recent discovery of fin infection in nature by the small hookless glochidium of *Unio gibbosus*, which has a larval thread.

I have rarely seen natural infections of gills by hooked glochidia; in two cases they were evidently unsuccessful, the glochidia having died, and were embedded in hypertrophied tissue at the base of the gills, apparently in process of shedding. The third and fourth instances were apparently successful infections of single glochidia, in one case on the heavy gills of a catfish, *Leptops olivarus*, and in the other on the sturgeon.

Another case was a heavy infection on the gills of *Pomolobus chrysochloris* by a glochidium which is hooked, but the hook is not

of the ordinary type in the Anodontinæ (see pl. IV, fig. 27). The hook has the character of a straight thong inside the apex of each valve. The glochidium has been identified as that of *Unio crassidens.* .

The absence of evidence of natural infections from certain species of mussels and failure to obtain infections with them according to known methods has led to the search for them as internal parasites of fishes. My examination of the alimentary tract of fishes has given negative results entirely. Mr. T. Surber, after infecting with *Quadrula trigona*, found their glochidia in the intestine 17 hours later, but they were not encysted, and the supposition was that they were not established in any way.

Type of cysts.—The type of cyst varies in different cases, and the question arises as to what are the factors that determine the form of a cyst. In artificial infections on several species of fish the cyst in each fish will vary in form as well as in distribution upon the gill in each species, and again infections with different species of mussel will vary in the same species of fish. That is, stimulus and reaction vary with the parasite and host. This is perhaps self-evident, and as a rule differences are not striking, but as there are occasional cases of marked peculiarity in cysts their consideration may be of interest. In the discussion of *Quadrula ebena* I have described the relatively large cysts. This holds for the natural host, *Pomolobus chrysochloris*, as well as for artificial infections on other species. The large glochidium of *Q. heros* has a relatively thin cyst in gill infections. In the case of *Q. pustulosa* the glochidium is usually quite deeply imbedded, but the cyst does not markedly change the contour of the gill filaments. This is due in part to the manner of implantation of the glochidium, it being usually attached to the edge of the broad filament in the catfish. There is commonly an inset of the cyst (pl. III, fig. 23) that seems peculiar to this form, but is not constant. Abnormal cysts of strange forms are occasionally found. I have figured one of these (pl. III, fig. 20), in which the hypertrophied tissue is more extensive than usual and prolonged into fingers or rays. In that shown in figure 20 the stimulation of the glochidia implanted at the base of the folds of the filament affected apparently the fundament of the folds, and thus we have a number of new folds produced. Studies of cyst formation, normal and abnormal, should have a practical value in determining the conditions governing retention of glochidia.

Seasons of infection.—The time of infection must of course be limited to the breeding season of the mussels, but as the period of breeding covers months in both the long and the short period types, the more exact fixing of the time of infection may be important. I have already discussed the question in connection with *Q. heros*, as to

whether infection takes place in the autumn or spring. Lillie (1895) intimates that there is some development of the larvæ during the winter in the case of the long-period breeder *Anodonta cataracta*.

Lefevre and Curtis (1912) assume that development for anodontas is complete in the autumn. Harms (1909) suggests the probability of two broods in the short-period breeder, *M. margaritifera*, during July and August. Conner (1909, p. 112) gives the breeding period for this species as June and August. I have seen indications of two broods in the breeding of *Q. ebena*, and Lefevre and Curtis (1912, p. 114) mention similar observations. The settlement of this question would require the keeping of females under observation during the breeding period, but there is the difficulty that no one, so far as I know, has yet succeeded in getting these mussels to breed in captivity.

I have reported the absence of infections by *Q. pustulosa* after September 1. It is probable that September marks the limit of infections by short-period breeders. The finding of infections by long-period breeders early in the autumn and spring upon the sturgeon, *Scaphorhynchus platorhynchus*, and the wintering of *Q. heros* upon its host show that infections are not confined to late spring. It is to be expected that the period of infection would be adapted in large measure to the habits and seasonal migrations of fishes.

In general we may say that for most mussels in this climate the season of infection comes in the warmer months. In southern waters as much restriction would not be expected.

Metamorphosis during the parasitic stage.—The development of the young mussels in the post-embryonic or parasitic period has been systematically worked out in a number of forms (Brown, 1878a, 1878b, 1884, 1889; Schierholz, 1888; Harms, 1907a, 1907b, 1907c, 1908, 1909; Lefevre and Curtis, 1912). I wish here to call attention to some apparently decided differences in extent of development observed in natural infections. Differences in the amount of development of the larvæ at the end of the period of parasitism are very strikingly shown in a comparison of such species as *Lampsilis ligamentina* and *Lampsilis lævissima* (Coker and Surber, 1911). In the case of the former the juvenile mussel leaves its host with no shell beyond that of the glochidium (Lefevre and Curtis, 1912); in the latter there is a relatively enormous growth. This extra-glochidial growth I have observed in the following: *Lampsilis lævissima, L. alata, L. gracilis, Plagiola donaciformis, P. elegans* (Howard, 1912), and *Quadrula pustulosa*. The growth in the case of the large glochidia of *L. alata* (pl. IV, fig. 28) and *Q. pustulosa* (pl. III, fig. 19) is only sufficient to give the form of the shell of the adult mussel to the juvenile. In the others, which have very small glochidia, the great growth during the parasitic period would seem to be a compensatory

provision giving them the size of other juveniles when taking up the post-parasitic life. It would not be surprising if in the case of the latter the metamorphosis were carried further than in those forms which have no growth beyond the glochidial shell.

Duration of the parasitic period.—Periods of parasitism have been reported (Lefevre and Curtis, 1912, p. 168) as short as 12 days, and I have observed a period as long as six months in the case of *Q. heros* carried through the winter. These cases were observed in artificial infections. In natural infections I have seen evidence of a long period in mussels carried by the sturgeon, *Scaphorhynchus platorhynchus;* matured larvæ were seen in late season catches, while none were seen in those taken through April and most of May or in October. Lefevre and Curtis have called attention to the lack of correspondence between their results and those of other observers (Harms, 1907, 1909; Schierholz, 1888) as to the effect of temperature on the length of parasitism. Considering the great variation in the period of metamorphosis for different species, I think it is obvious that the influence of temperature could be determined accurately only in a single species or in species having the same period. Individual variation in the length of period for mussels which were implanted at the same time on the same fish Lefevre and Curtis explain as due to differences in nutrition of the larvæ.

Larval thread.—The presence of a thread gland and larval thread in the mature glochidium I have reported and described under *Quadrula heros* and *Quadrula plicata*. Lefevre and Curtis (1912, p. 151, 152), in a thorough discussion of this interesting organ, in which they state that they have found it only among the Anodontas and Unios, agree with Lillie (1895) that it is an excretory organ and the thread is an excretion primarily. They do not agree with Schierholz (1888) in considering the thread an efficient organ for aiding in attachment to fishes. In this connection it is interesting to note that in this form, which is the only one of its kind known to take the habit of external or fin infection, we have an organ that is characteristic of fin-infecting groups, *Anodontas* and the European *Unios*. Since making this observation on *Q. heros* I have noted the thread gland in *Unio gibbosus* and also observed this glochidium in natural infection upon the fins.

From these observations it looks as if this habit might have some bearing on the function of the thread gland. Here we have among the hookless glochidia a form showing the thread gland and thread more highly developed apparently than in the Anodontas. The inference is natural that the thread has some function other than excretion alone. If a fundamental embryonic (Lillie, 1895) organ present at some time in the development of all glochidia, its persistence to the mature state in some cases and not in others would

seem to indicate that its function later is not of a fundamental nature like excretion or it would persist in all. Lefevre and Curtis advance the argument that the threads are dissolved in a day or two and so are not effective during the greater part of the period in which the glochidia may be on the bottom. This would make no difference if infections take place at the time the glochidia leave the mussel, the evidence for which I have discussed above. (See conditions of infection in nature, p. 39.)

Absence of parasitism.—The interesting discovery of metamorphosis without parasitism as reported by Lefevre and Curtis (1912) for *Strophitus edentulus* (Say) suggests the possibility of some similar explanation for the absence of evidence of infection by some common species. This is especially to be looked for in species which have conglutinates similar in character to those of *S. edentulus.* I have in mind those of *Obliquaria reflexa* (Rafinesque). The fact that infections of this species have not been found lends support to the supposition that there is possibly something unusual in their life history.

Another species of mussel for which no natural infections have been reported is *Anodonta imbecillis.* While making measurements of the glochidia from a number of gravid individuals of this species collected during the month of November, I noticed that in many cases what I had supposed at first glance were mature glochidia were in fact juvenile mussels with organs developed to the stage usually seen in juveniles at the time they leave their host. These young mussels lie crowded in the marsupial gills of the parent without any conglutinate structure whatever. The outer gills, as in other anodontas, are marsupial, and these become well distended throughout their whole length when gravid.

In regard to the breeding of this species, Ortmann (1912) says it is gravid from September to May. My observations, which are rather limited, I give below:

Fairport, Iowa, July 16, 1910, 1 with glochidia.
Fairport, Iowa, May 13, 1912, 1 with glochidia.
Fairport, Iowa, May 27, 1912, 1 with early embryos.
Moline, Ill., September 24, 1912, 1 not gravid.
Moline, Ill., November 7, 1913, 2 with early embryos; 1 with both late embryos and glochidia, and 6 with juveniles.

In addition to these I have found numbers of free juveniles ranging from 5 to 30 millimeters not sexually mature. These stages are remarkable for the thinness of their shells and the flatness of the mussel as a whole. The term "floater" of the mussel fishermen for this type of mussel is well applied in its use for this species.

The presence of juveniles during November in the gills of a majority of the specimens examined seems to indicate that metamorphosis is

probably completed in the fall. The time of discharge of the young mussels is yet to be determined, but the appearance of glochidia again in early spring would seem to indicate that the juveniles escape in the fall or early winter.

Among the six lots of marsupial juveniles that I collected, the degree of development varied slightly as to amount of shell growth, otherwise there seemed to be little difference. This growth consists of a narrow rim only around the edge of the glochidial shell. The hooks of the glochidium are still much in evidence but are much weaker than in parasitic forms. A noticeable feature is the large proportion of gaping shells as compared with a similar lot of glochidia. It would seem that with the loss of the powerful single adductor muscle the action of closing is less vigorous. Between the gaping valves can be seen the ciliated foot, on each side the gill papillæ, two adductor muscles, mantle, etc., indicating a development equal to that of other young Naiades at the end of parasitism.

I have tested the reaction of the glochidia in the presence of fish and obtained strong evidence that they do not respond as other known parasitic forms. Mature glochidia taken in March were employed. In an exposure to fish for an hour they failed to give the usual infection. A few glochidia lodged in the mouths of the fish, but no encystment could be detected. The fish showed no response. Following this test the fish were exposed for 10 minutes to the glochidia of *Symphynota complanata* (Barnes.) These rapidly became attached and the fish showed considerable uneasiness, in marked contrast to their indifference in the presence of the other glochidia.[a]

From these observations I think I am warranted in concluding that this mussel passes through its metamorphosis without parasitism. The absence of a conglutinate (Lefevre and Curtis, 1912) or placenta (Sterki, 1898) is of interest, as we have here a case of nonparasitic development independent of this type of structure found in Strophitus.

It is a question whether the development, following the escape of the glochidium from the egg, is aided by absorption of food or not. One would expect the former, as it is evident that this species has descended from parasitic ancestors which received extraneous nutrition during the parasitic period.

The discovery of the absence of parasitism in this species already possessing the distinction of being hermaphroditic certainly adds to its reputation as an eccentric among its relatives in the Unionidæ.

[a] Observations made since the above was written indicate that juveniles may be found in the marsupium at almost any time during the year. I have also been able to secure infections and encystment on fishes with *Anodonta imbecillis* as well as *Strophitus edentulus*. In the latter complete metamorphosis was observed. Thus for *edentulus* we have indicated facultative parasitism, while in the other we have a persistence of the parasitic reaction at least when artificially brought in contact with a host. Metamorphosis on fishes was not secured in *A. imbecillis*. Abundant additional evidence is at hand that development in this (*imbecillis*) species normally proceeds without parasitism.

JUVENILE STAGE.

The period in the life of the mussel following the parasitic stage has been given comparatively little attention by investigators. It is commonly stated that the mussel upon leaving the host assumes the adult form and manner of life. The investigations made upon this stage, however, indicate that the differences are probably of practical importance; that the adult form is not completely attained for some time (Schierholz, 1888), and that the manner of life may be quite different. According to Schierholz (1888, writing of the Unionidae):

> The following organs are acquired during this stage: The siphons, "Lippentaster," outer gills, and sexual glands. In *Anodonta* the outer gills are acquired the second summer, in *Unio* the third and fourth summer, while the sexual glands are developed in *Anodonta* the third summer and in *Unio* the fourth and fifth summer.

The acquirement of the sexual glands would mark the adult condition and the end of the juvenile period. The size upon first attaining the adult condition would, of course, vary considerably in individuals as well as in species. The smallest gravid mussels I have secured were 13 mm. in length. This was in the very small species *Plagiola donaciformis*, in which an example 50 mm. long would be exceptionally large.

The washboard (*Quadrula heros*), the largest of American mussels, has shell markings on the umbones that seem to be characteristic of the juvenile. These sculpturings mark the shell up to a size of 50 mm. to 60 mm., when they often cease abruptly. The size at maturity, according to the evidence I have, would be much greater, as the smallest breeding individual that I have collected was 91 mm. long. This showed a growth of three years beyond the juvenile shell and a total age estimated at 8 years.

In statistical estimates in ordinary sized species I have taken the arbitrary length of 20 mm. (Lefevre and Curtis, 1912) as a limit for the early juvenile stage. For large and small species it is evident this length would not be sufficiently accurate.

The sculpturings mentioned above for *Q. heros* are characteristic of the juveniles of most species, although they are absent in some. Commonly they are limited to the earlier portions of the shell.

The presence of a byssus in many species, as reported by Sterki (1891), Frierson (1903), White (1905), and Isely (1911) and the attachment of the young mussels to stones and gravel in shallow water I have been able to confirm in a number of cases, though, excepting *Q. plicata*, not among the *Quadrulas*. This habit of attachment in shallow water is found among the *Lampsilis* group, which in the adult stage are comparatively active mussels commonly in deep

water. This is a noteworthy contrast between young and adult as to habits and habitat.

In my investigations upon the juveniles I have not found the early stages as uncommon as the literature led me to expect (Lefevre and Curtis, 1912, p. 177). The clammers of the Mississippi River seem to be familiar with them, reporting that they often bring them up with the "spider web attached," referring to the byssus threads. Their small size makes them less conspicuous, and special apparatus is required for collecting them. In 1912 I found about 400 juveniles under 20 mm., exclusive of *Plagiola donaciformis*, and comprising 25 species.

Among the *Quadrulas* I have not found so great a difference, as a rule, in the habitat of juvenile and adult as Isely (1911) has reported for the Lampsilinæ (Ortmann). However, in species which show marked differences between juvenile and adult it is quite evident that in any scheme of propagation which would carry the young through this stage special consideration must be given this period of the life history.

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EXPLANATION OF FIGURES.

Photographs and drawings by the author, the drawings being made with the aid of a camera lucida.

PLATE I.

Fig. 1. *Quadrula pustulosa* (Lea).   Interior of right valve.
Fig. 2. Same individual.   Exterior of left valve.
Fig. 3. Juvenile of same species.
Fig. 4. *Quadrula metanevra* Rafinesque.   Interior of right valve.
Fig. 5. Same individual.   Exterior of left valve.
Fig. 6. Juvenile of same species.
Fig. 7. *Quadrula ebena* (Lea).   Interior of right valve.
Fig. 8. Same individual.   Exterior of left valve.
Fig. 9. Juvenile of same species.
Fig. 10. *Quadrula trigona* (Lea).   Interior of right valve.
Fig. 11. Same individual.   Exterior of left valve.
Fig. 12. Juvenile of same species.

PLATE II.

Fig. 13. Juvenile of *Quadrula heros* (Say).
Fig. 14. Adult of same species.   Left valve.
Fig. 15. The same species.   Interior of right valve.
Fig. 16. Juvenile of *Quadrula plicata* (Say).
Fig. 17. Adult of same species.   Exterior of left valve.
Fig. 18. The same species.   Interior of right valve.

PLATE III.

Fig. 19. Glochidium of *Quadrula pustulosa* implanted upon the gill of *Ictalurus punctatus;* a natural infection taken August 26.   Considerable development is evident from the growth of shell at the edge of the glochidial valves (*e. g. s.*) and two adductor muscles (*Ad. m.*) and foot (*fo.*) that are visible.   The blood vessels (*B. V.*) of the fish's gills are seen to be inclosed by the valves of the glochidium.   This is the same glochidium as that shown in figure 23.

Fig. 20. An abnormal cyst produced by the glochidium of *Quadrula pustulosa* upon the gill of *Ictalurus punctatus.*

Fig. 21. Glochidium of *Quadrula heros* showing the larval thread (*l. t.*) and larval thread gland (*lt. g.*) clearly differentiated by staining in borax carmine.   The adductor muscle (*Ad. m.*) lies in the center.

Fig. 22. Glochidium of *Quadrula heros* with gaping valves seen from a side view. The larval thread (*l. t.*) is to be seen between the valves and its point of emergence ventral to the adductor muscle.   Inner and outer sensory hair cells (*s. h. c.*) are visible on each valve.

Fig. 23. Filament of gill of *Ictalurus punctatus* naturally infected by the glochidium of *Quadrula pustulosa.*   The cyst is set off on each side by incisions of the filament. This is somewhat characteristic of gill cysts in this species though not constant.   The same glochidium is shown in figure 19.

Fig. 24. Encysted glochidium of *Quadrula ebena*, artificial infection upon *Micropterus salmoides.*   The large size of the cyst is to be noted as characteristic of infections with this species of glochidium.

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Fig. 25. A dorsal view of a juvenile of *Lampsilis alata*, 9 mm. long, showing the glochidial shell still visible.   Magnification, 18 diameters.

Fig. 26a. A cluster of glochidia of *Quadrula heros* (Say), imbedded in the pectoral fin of a sheepshead, *Aplodinotus grunniens*.   The fish was infected artificially October 7; these glochidia were removed by clipping off a small portion of the fin April 18. The soft parts are sufficiently distinct to permit the determination of the amount of metamorphosis which is nearly completed.   Differences in appearance of the individuals are due chiefly to their varied orientation.   The narrowest figure is an optical section taken in a transverse plane at right angles to the longitudinal axis.   The preparation was stained by Mayer's hæmalum.

Fig. 26b. Gill filament of a sunfish, *Lepomis pallidus*, artificially infected by the glochidium of *Quadrula heros*.   Age (Dec. 6), 69 days.   The presence of two adductor muscles indicates that some metamorphosis has taken place.   The cyst is seen to be thin as compared with some other species.   Drawn in a living condition immediately after removal of the filament from the gill of the fish.

Fig. 27. Natural infection of the herring, *Pomolobus chrysochloris*, by the glochidia of *Unio crassidens*.   This fish was captured May 16.   The figure represents the tip of a filament shown chiefly in outline by dotted lines.   The cyst includes a number of the finer subdivisions of the filament each with its afferrent blood vessel.

Fig. 28. A natural infection of the sheepshead, *Aplodinotus grunniens*, by *Lampsilis alata*.   Considerable growth of shell is to be seen beyond the valves of the glochidium while still imbedded in the tissue of the host.

PLATE V.

Glochidia of species of *Quadrula*.   All figures are magnified 275 diameters.

Fig. 29. *Quadrula lachrymosa* (Lea).   A little immature; left valve, showing large mantle cells just beneath the very transparent shell and large adductor muscle.

Fig. 30. *Quadrula ebena* (Lea).   Surface view of right valve, showing adductor muscle and pores of shell.

Fig. 31. *Quadrula metanevra* Rafinesque.   Surface view of left valve.

Fig. 32. *Quadrula plicata* (Say).   Right valve, showing thread gland passing around the adductor muscle and thread issuing posterior to the muscle.

Fig. 33. *Quadrula trigona* (Lea).   A surface view of the right valve.

Fig. 34. *Quadrula solida* (Lea).   A surface view of the left valve.

Fig. 35. *Quadrula heros* (Say).   The left valve with the focus of the microscope slightly below the surface.   The large light circle is the expanded portion of the thread gland.   The shaded area represents an organ whose function has not been determined.   A similar structure is visible in figs. 30 and 32; in the latter it appears to be continuous with the thread gland.

Fig. 36. *Quadrula pustulosa* (Lea).   Left valve; surface view.

PLATE VI.

Fig. 37. *Quadrula pustulata* (Lea).   Interior of the right valve.

Fig. 38. The same species.   Left valve.

Fig. 39. Juvenile of the same species.

Fig. 40. *Quadrula granifera* (Lea).   Interior of the right valve.   The dark shade is due to the purple nacre of this shell.

Fig. 41. The same species.   Left valve.

Fig. 42. Juvenile of the same species.

Fig. 43. *Quadrula lachrymosa* (Lea).   Interior of the right valve.
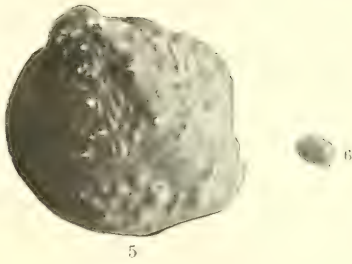
Fig. 44. The same species.   Left valve.

Fig. 45. Juvenile of the same species.

Fig. 46. *Quadrula solida* (Lea).   Interior of the right valve.

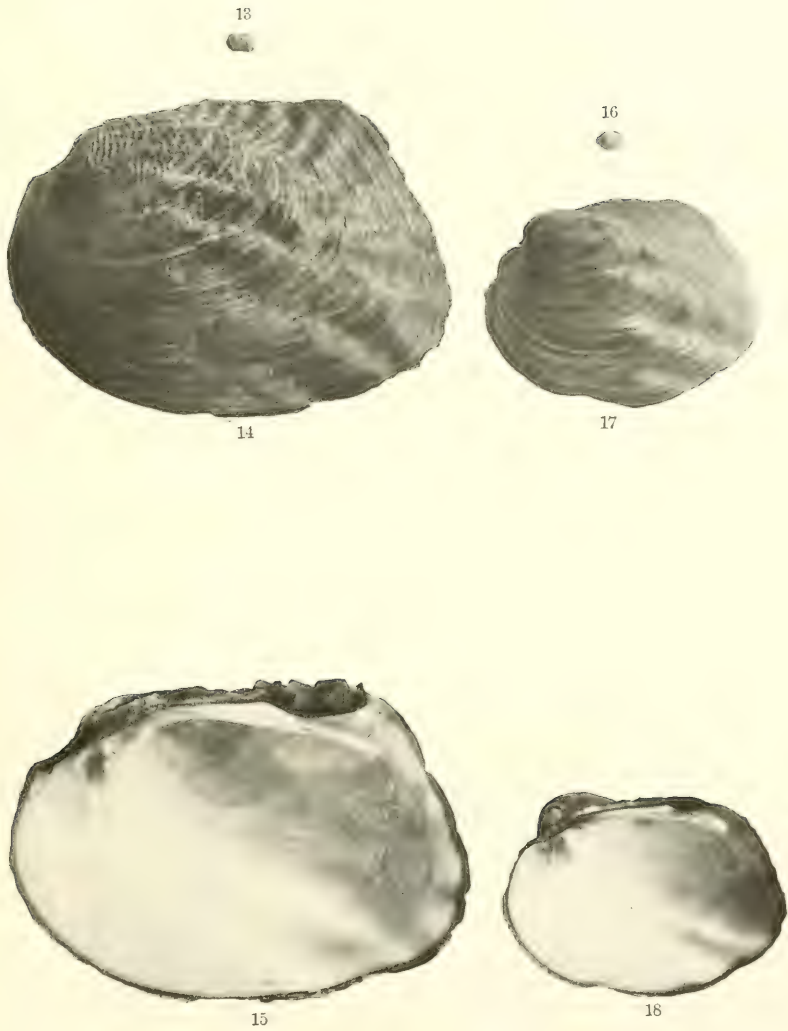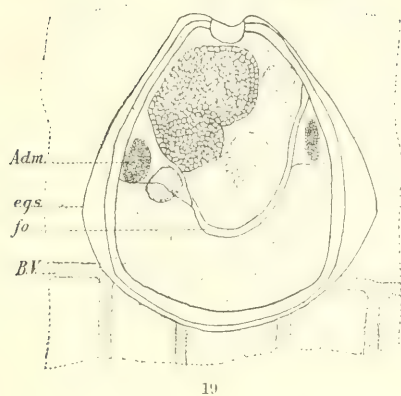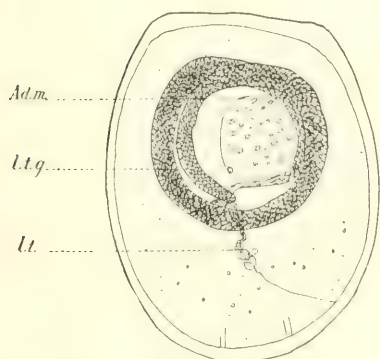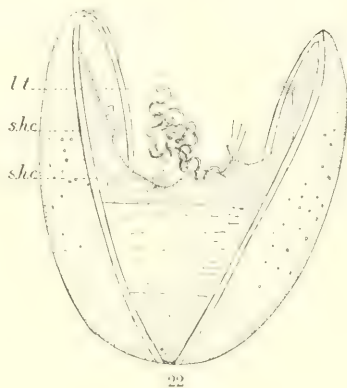Fig. 47. The same species.   Left valve.

PLATE I.

PLATE II.

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PLATE III.

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PLATE IV.

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PLATE V.
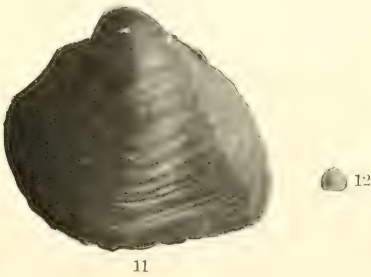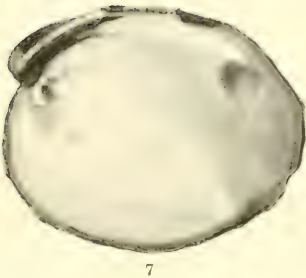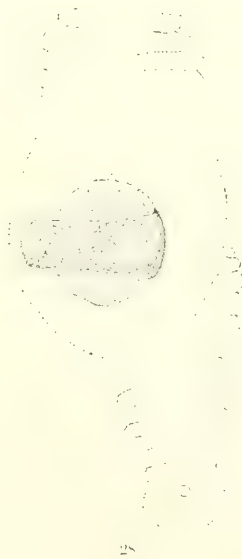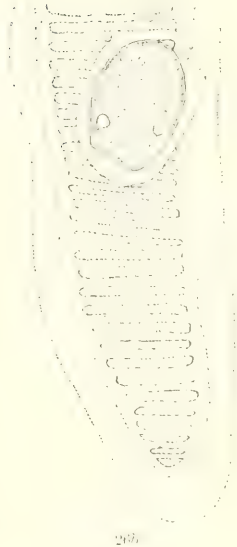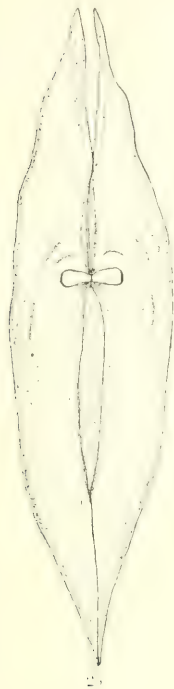
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PLATE VI.
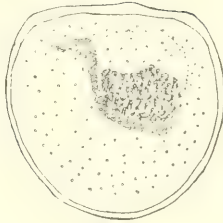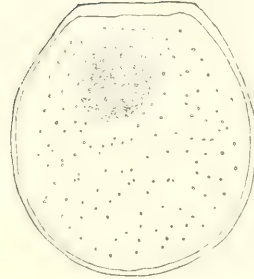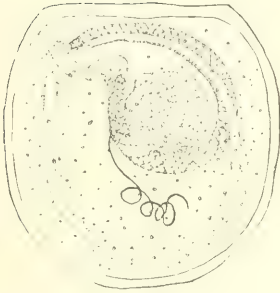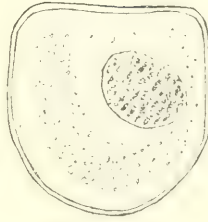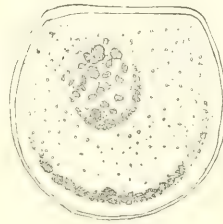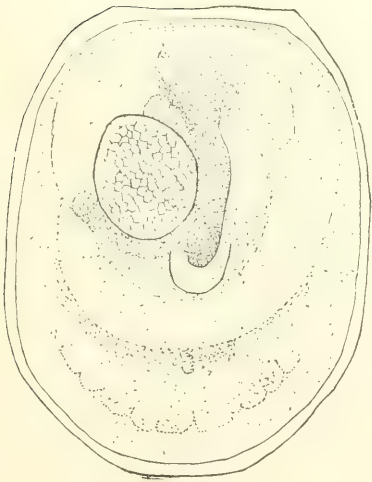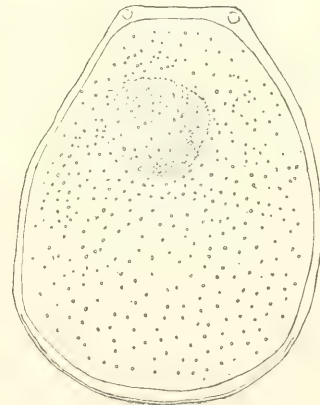
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